BOLL ABSCISSION AND FIBER PROPERTIES IN UPLAND COTTON AS INFLUENCED BY NITROGEN, MOISTURE, AND GIBBERELLIC ACID TREATMENTS

by

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I hereby recommend that this dissertation prepared under my direction by Rex Weldon Millhollon

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INTRODUCTION

For many years cotton growers and researchers have been concerned with the large number of bolls that are abscissed (shed) during the growing season. Such a loss of organic material is serious, since each boll that is abscissed represents wasted metabolic energy that could be more effectively used by the plant.

The importance of this problem is evidenced by many experiments which have been conducted to study boll abscission in cotton. These experiments have furnished a great deal of knowledge about this subject, but none of them has been successful in tracing the pathway that leads to the abscission of bolls. Thus, a prominent worker in this field recently concluded that "the cause, or causes, of boll shedding are unknown" (18).

After a thorough literature review, the following broad areas were chosen for a detailed investigation of the boll abscission phenomenon in cotton:

(1) The effects of nutrition and growth on boll abscission and fiber properties as reflected from moisture and nitrogen treatments.

(2) The effects of a growth regulator, gibberellic acid, on boll abscission and fiber properties.

(3) The role of pollination and embryo development in the abscission process.

(4) The role of natural auxin in the abscission process.

LITERATURE REVIEW

Three excellent literature reviews have appeared recently which cover various theories and studies to explain the abscission of buds and bolls of cotton (1, 18, 22). The importance of cotton boll abscission is indicated by the extensive literature pertaining to this subject. Since the fruiting process seems to be intimately correlated with growth, literature on morphology, growth, and general nutrition of the cotton plant will be briefly reviewed in addition to literature on boll abscission and fiber properties.

Morphology and General Growth of the Cotton Plant

The cotton plant is characterized by a long tap root, indeterminate shoot growth, and dimorphic branches. During growth of the main stem axis, two types of buds are formed at the base of the leaf at each node. One is a true axillary bud, and one is to the side of this bud and is referred to as the extra-axillary bud (9). True axillary buds may develop into vegetative branches which are morphologically like the main stem, and extra-axillary buds develop into fruiting branches which give rise to floral buds at each node. Commonly, only one axillary bud

develops into a branch at any one node, but both types of buds may initiate growth at the same node late in the season (28). Vegetative branches usually develop only on the lower first few nodes, varying with such factors as spacing and variety, while fruiting branches develop at nodes higher on the plant. Once development of fruiting branches has been initiated, a fruiting branch will be formed approximately every 3 days, and flowers will appear approximately every 7 days on successive nodes of an actively growing fruiting branch in Acala cotton (41).

Fruiting branches are quite distinctive due to their nearly horizontal position and zig-zag arrangement of their growth. According to Gore (21) this characteristic is due partially to a sympodial type growth which results when the terminal bud of a fruiting branch differentiates into a floral bud at a node. Continued growth of the fruiting branch is made possible by a zone of meristematic tissue which begins to grow between the newly differentiated flower bud and the leaf at a node. This zone of tissue develops two growing points. One of these becomes the axillary bud of the node, and the other continues the growth of the fruiting branch. Continuation of this type of sympodial growth results in a fruiting branch composed of a series of axis or internodes which are terminated by flower buds.

Axillary buds of fruiting branches of Acala cotton are usually dormant according to King (32). However, he noted that they are

stimulated to grow when an excessive number of flower buds are removed either by natural abscission or by artificial means. When stimulated, these buds grow into very short vegetative branches which in turn produce very short fruiting branches.

Floral buds usually require about 21 days to mature into a flower (5). At anthesis a large showy hypogynous flower is produced with 3 leafy bracts, 5 small green sepals (lobed), 5 large petals (fused at base), and numerous stamens (90 to 100) which are attached to a staminal column around the pistil. The pistil of upland cotton consists of four to five united carpels with 8 to 10 ovules per carpel (28, 48).

Pollination usually takes place on the morning of anthesis and fertilization is completed approximately 30 hours after pollination (20). The first division of the endosperm occurs shortly after fertilization is completed, but the zygote does not divide until approximately 72 to 90 hours after anthesis (3, 44). The boll develops rapidly after fertilization and matures approximately 45-60 days after anthesis. However, Hawkins and Serviss (25) found that fiber from bolls of Acala cotton formed during September required approximately 78 days to mature.

Boll Abscission

General

The preceding discussion has shown that a fruiting branch has the potential of producing a mature boll at each node. This potential is seldom realized, however, since a large number of both squares (floral buds) and bolls are abscissed at an early age. The magnitude of boll abscission is shown by the fact that 50 per cent or more of the flowers produced during a season are abscissed as young bolls (22). Although square abscission has not been studied as much as boll abscission, Loomis (35) reports an average of 45 per cent square abscission for Acala cotton grown in Arizona. One of the rather striking characteristics of square and boll abscission is the common observation that flowers at anthesis or approximately 2 days thereafter are seldom abscissed (34). On the other hand, squares apparently can be abscissed at any time up to anthesis, but according to Loomis (35) most squares are abscissed at an average age of 16 days. The age at which bolls are abscissed seems to be much more definite. Lloyd (34) and McNamara and Hooten (41) have shown that bolls are abscissed at an average age of 5 days after anthesis.

Several workers (35, 41, 49) have observed the somewhat zonal nature of square and boll abscission on the cotton plant. McNamara and Hooten (41), for example, found that the first node of the fruiting branches

produced over half of the total crop; and Loomis (35) found that the abscission percentage of both squares and bolls increased progressively from the first node to the last node on a fruiting branch. Thus, although squares and bolls may be abscissed at any node, the abscission trend is primarily upward and outward from the central axis of the plant.

Abscission Zone

The general area of the abscission zone is marked by a slight external groove at the base of the peduncle. The groove itself probably has no direct relationship with the abscission process (34). In Lloyd's (34) description of the abscission process he points out that although cell division is usually observed in the abscission zone, the digestion of the middle lamella and adjacent layers of cellulose wall are prerequisites for actual separation of cells. Abscission usually progresses transversely across the peduncle; and the bud or boll falls cleanly, leaving a prominent scar. In other cases, however, the abscission zone may occur at an oblique angle, and the bud or boll may dry up and hang on the plant for some time.

Water Relations

Most early workers attributed abscission to a lack or an excess of water as Hall (22) pointed out in his review of this subject. Balls (3), one of the earliest investigators of abscission, found that when a few roots

were severed, a stimulus was released which caused abscission in 4 days if the plants were left in sunlight; but no abscission occurred if the plants were shaded. He theorized that stomates close when roots are damaged, and abscission occurs due to a rise in leaf temperature.

The theory that water is the primary cause of abscission has generally been disproved by rigidly controlled irrigation experiments conducted by several workers (4, 10, 24). For instance, Hawkins (24) obtained very high abscission values of 58, 70 and 73 per cent for plants growing on a heavy soil with "dry," "medium," and "wet" irrigation treatments, respectively. Beckett and Dunshee (4) obtained similar high values of 82, 76, and 75. 7 per cent abscission for plants grown on a sandy soil with "dry," "medium," and "wet" irrigation treatments, respectively. Each of the preceding experiments shows differences in abscission percentage due to irrigations, but the extremely high values for all treatments illustrate the point that water per se is not the primary cause of abscission.

Hawkins et al. (26) found that relatively high osmotic pressure of the leaf sap of Acala cotton was always followed by less abscission. The hypothesis was advanced that abscission might be the result of a water deficit in the bolls due to a wide variation between the osmotic pressure of leaf fluids and that of bolls. This idea was refuted in a

later experiment (27) when abscission was observed to be higher when osmotic pressure values for leaves and bolls were closest together.

Nutritional Relations

Maskell and Mason (37) have shown that nitrogen moves to the leaves in the transpiration stream. In a summary of some of their earlier work Maskell and Mason (38) visualized a transport of nitrogen and carbohydrate compounds from the leaf along a diffusion gradient in the sieve tubes. They found that nitrates were assimilated to organic nitrogen in the leaves, and all fractions were translocated through the sieve tubes. Mason and Maskell (40) also found that reducing sugars were the main carbohydrate in the leaf, and sucrose was the main carbohydrate being transported to bolls and other parts of the plant.

One theory often used to explain boll abscission is the nutritional theory which probably started with Mason's (39) work in 1922. He felt that the plant could only retain as many bolls as it could supply with nutrients. The work of Hawkins et al. (26) seemed to substantiate this theory since they found that high carbohydrate levels in the plant were almost always followed by lower abscission rates, and vice versa. When all floral buds were removed as they formed, Eaton (12) and Eaton and Joham (13) found that the roots weighed three times more, contained three times more sugar, and absorbed 60 per cent more bromine than

the control. This seems to indicate that developing bolls use the available nutrients at the expense of roots, and eventually both mineral nutrients and carbohydrates become limiting factors in boll retention.

Crowther (10), Wadleigh (49), and Armstrong and Albert (2) observed the dominating influence of developing bolls on the supply of nitrogen of cotton plants. Increased use of nitrogen by bolls was usually made at the expense of leaves, and nitrogen treatments had very little effect on this relationship. Likewise, Crowther (10) observed that most of the total nitrogen in the plant was concentrated in leaves early in the season, but during boll development this relationship shifted until there was approximately 70 per cent of the total nitrogen in bolls and only about 15 per cent in leaves. Wadleigh (49) and Crowther (10) theorized that such a nitrogen balance was due to the incapacity of roots to take up adequate nitrogen because the roots were deprived of carbohydrates by developing bolls.

The nutritional theory was not substantiated in later work by Eaton and Ergle (17), since girdling and daily spraying with urea always increased abscission even though in most cases the carbohydrate and nitrogen content of the plant was increased by such treatments. Eaton and Rigler (14) observed that square abscission increased at a low light intensity which also decreased the carbohydrate content. However, the nutritional theory was again questioned since abscission occurred on

plants grown under high light intensity even though the carbohydrate level was not reduced to the level of plants grown under low light intensity. Eaton and Rigler (14) also observed that relative fruitfulness values (number of bolls per 100 grams of fresh weight of stems and leaves) were remarkably similar for plants grown on 4 levels of nitrogen in a nutrient solution even though growth was quite different.

From the type of evidence presented, Eaton (18) concluded that the nutritional status of the plant did not directly influence abscission. However, he conceded that "without the protective mechanism of boll shedding, the cotton plant would undoubtedly overfruit and, in accord with the behavior of many horticultural plants, produce smaller fruit with the probability of poor fibers."

Environmental Relations

Ewing (19) was one of the first workers to try to relate environmental factors to boll abscission. After two years of observations, he came to no definite conclusion concerning the influence of soil moisture, relative humidity, or air temperature on abscission. On the other hand, Dunlap (11) found that drought accelerated abscission while temperature seemed to have little effect.

Dunlap (11) and Eaton and Rigler (14) studied the effect of light intensity on abscission and found that fruit abscission was accelerated by low light intensity. However, carbohydrates were also reduced;

therefore, low light intensity may have had an indirect effect on abscission.

Growth Regulator and Auxin Relationships

Since growth regulators have been used to retain fruits on many types of fruit trees, Eaton (15) studied the effect of certain chemicals on boll abscission in cotton. Plants were dusted with 100 ppm sodium 4-chlorophenoxyacetate and 100 ppm naphthaleneacetic acid in combination and separately, but no measureable increase in boll retention could be detected. Walhood (50) sprayed whole cotton plants with 100 ppm indoleacetic acid (IAA) at weekly intervals during July and August and found that boll retention was significantly increased for flowers which were at anthesis on the day of treatment. However, this increase was followed by less retention between sprayings so that there was no difference in total boll retention for the season.

Walhood (51, 53) found that boll retention could be increased to almost 100 per cent when 0.25 ml. of gibberellic acid (GA) was applied to the calyx cup of 1-day-old bolls. The effectiveness of GA usually decreased as boll load increased, but retention was still higher than the check. Gibberellic acid was effective at concentrations from 1 ppm to 1,000 ppm, but 100 ppm seemed to be the optimum concentration. Since GA usually increased the growth rate of young bolls, the possibility that increased retention was actually due to increased production of natural

auxin was also considered. However, when IAA was applied to calyx cups, boll retention was decreased rather than increased. The possibility that GA is responsible for increased auxin production is still not refuted, however, since Homan (29) found that dwarf corn seedlings treated with GA grew normally and produced nearly twice as much auxin as the control. On the other hand, dwarf seedlings treated with IAA were not affected. The possibility of an interaction between GA and IAA was not found and Homan concluded that GA was actively associated in some way with auxin production in the plant.

The effects of GA are not limited to boll retention in cotton; but as observed on many other plants, GA also stimulates vegetative growth. Walhood (52) found that growth of cotton was proportional to the number of applications of GA made to the apex of the plant, but reduction in boll size usually accompanied this increased growth.

Carns (7) and Carns et al. (8) have isolated a hormone from carpillary tissue of young bolls that accelerates abscission. The concentration of this hormone was found to increase to the time of greatest boll abscission. It was extracted with a petroleum ether fraction and moved to an area between Rf 0.6 and 0.9 on a chromatogram. This hormone inactivated auxin activity and promoted abscission when applied to young cotton bolls. These authors felt that this hormone plays an important role in boll abscission by interacting with naturally occurring auxin.

Fiber Properties

General

Hawkins and Serviss (25) studied the development of the cotton fiber in detail. They found that fibers start to elongate shortly after flowering, and elongation proceeds rapidly after fertilization until a maximum length is obtained in about 21 days in Acala cotton. Thickening of fiber walls begins shortly before elongation ceases and is completed 48 to 75 days after anthesis. The rate of fiber-wall thickening decreases as the season progresses and temperatures become lower.

Brown and Ware (5) have described some of the general properties of the cotton fiber. Secondary wall layers which determine important fiber properties are almost pure cellulose, and these layers provide strength since they are laid down in spirals at an angle to the long axis of the fiber. Fiber fineness is an important characteristic which influences the number of neps in cloth. Fineness is determined by the thickness and perimeter of the fiber wall and is thus closely related to fiber strength and maturity. Fiber length, strength, and fineness are inherited characters but may be greatly influenced by environment.

Factors Affecting Fiber Properties

Most of the studies of fiber properties have dealt with water and fertilizer variables in combination or separately. Reports on the influence of nitrogen on fiber properties are somewhat contradictory.

Crowther (10) reported a very significant increase in fiber length due to increased nitrogen supply, but the work of Wadleigh (49) and Hamilton et al. (23) indicated that fiber length was unaffected by nitrogen treatments. Hamilton et al. (23) found that a nitrogen deficiency decreased such factors as boll size, number of seeds per boll, seed index, lint index, and fiber fineness. Wadleigh (49) also noted that a nitrogen deficiency decreased most factors, but he found that the number of seed per boll was unaffected while lint percentage was increased.

In general, drought increases fiber strength and decreases such factors as boll size, seed index, lint index, fiber length, and fiber maturity (16, 47). Eaton and Ergle (16) found that fiber strength increased when available carbohydrates increased as a result of drought or defloration.

In a recent paper, Stockton and Walhood (46) suggested that irrigation treatments may only have an indirect effect on fiber properties. They noted that temperature increased under the plant canopy as irrigation frequency decreased. In an experiment in which bolls were covered with white and black cloth, they found that an increase in boll temperature due to the black cloth was usually accompanied by finer fiber, smaller boll size, and shorter fiber length. Since irrigation treatments usually alter the growth pattern of the cotton plant, bolls from different irrigation treatments may also mature under different temperature conditions; and thus temperature may actually be responsible for observed differences in fiber properties.

MATERIALS AND METHODS

The experiments for this study were conducted over a two-year period during 1959 and 1960. All field experiments were conducted at the University of Arizona's Cotton Research Center, Phoenix, Arizona. The experimental field used during 1959 was adjacent to the one used in 1960. The soil type of both experimental fields was Adelanto clay loam. Soil variation existed due to heavy cut and fill areas which were required to level the fields during the winter of 1957-1958. Acala 44 cotton, a variety of Gossypium hirsutum L., was planted on 40-inch rows on April 8 in 1959 and 1960. A rigid insect-control program was followed throughout the season during both years. Inadvertently, plants were defoliated on October 24 in 1959, but no defoliant was applied in 1960. Otherwise, standard cultural practices were followed with the exception of treatment variables.

The experimental design for 1959 was a 3 by 3 factorial arranged in a stripped split-plot design with 7 replications. Irrigation treatments were whole plots arranged in strips, and nitrogen treatments were sub-plots arranged in randomized blocks within each irrigation level.

The experimental design for 1960 was similar to that of 1959 with the exception that a gibberellic acid treatment was added to make a 3 by 3 factorial arranged in a stripped split-split-plot design with 6 replications. Gibberellic acid treatments were sub-subplots arranged in randomized blocks within each nitrogen level.

These designs provided good precision for testing the main effects of nitrogen and gibberellic acid treatments. Irrigation treatments were stripped, and the main effect of these treatments could not be tested since there was no valid error term. However, all treatment interactions were tested with good precision.

Plots used to obtain yield data in 1959 were four rows wide and 50 feet long. In 1960 the length was reduced to 25 feet to facilitate handling. All data were taken from the two inside rows; the two outside rows were buffer rows. Detailed observations on treatment effects were made on 25-foot plots which were located directly behind the plots used to obtain yield data. In each of these plots four representative and uniformally spaced plants were selected from the center two rows for a detailed study of flowering and boll abscission. These observation plots were replicated four times for each treatment.

Open flowers were tagged daily by attaching a small dated tag to the peduncle, and the number of tags used daily in each plot was recorded. Tagging was started the latter part of June when flowering

was initiated and was stopped September 23 in 1959 and September 10 in 1960. Tags that remained on plants at the end of the season were collected, and a daily record of boll retention was made. Height measurements were also made on two representative plants per plot on July 13 and August 24 in 1960. Measurements were made of the length from the first node to the tip of the main stem.

Fiber properties were determined from 25 boll samples collected from the two center rows before each of three picking dates on September 22, November 9, and January 7 in the 1959 experiment; and September 26, November 5, and December 16 in the 1960 experiment. Most of the bolls picked at each date had flowered during June and July (1st date), August (2nd date), and September (3rd date). Standard fiber analyses were made in the University of Arizona's Cotton Laboratory at Tucson. Length, strength, and fineness were measured using the Fibrograph, Pressley strength tester, and Micronaire, respectively, as described by Brown and Ware (5)

Soil Moisture Treatments

Moisture treatments were divided into dry (I-D), medium (I-M), and wet (I-W) treatments as measured by gravimetric methods. The dry, medium, and wet treatments were irrigated when approximately 80, 60, and 50 per cent available moisture was exhausted from the surface three feet of soil, respectively. All treatments received a preplanting irrigation, and all subsequent irrigations were applied in quantities to

wet the entire root zone. Water was supplied by furrow irrigation in all cases. Irrigation treatments in 1959 were initiated immediately after the preplanting irrigation; and after this irrigation the I-D, I-M, and I-W treatments received a total of 4, 6, and 7 irrigations, respectively. In 1960 all treatments received common irrigations on May 22 and June 15 after the preplanting irrigation before irrigation treatments were initiated. This was done to insure an equal response to the anhydrous ammonia application for all treatments. A total of 5, 6, and 7 irrigations were applied (excluding the preplanting irrigation) on the I-D, I-M, and I-W treatments, respectively.

Nitrogen Treatments

A single application of 0 (N-0), 100 (N-100), and 200 (N-200) pounds of nitrogen was applied as anhydrous ammonia on June 12 in 1959 and June 14 in 1960. Anhydrous ammonia was injected into the soil about 10 inches to one side of the row of cotton at a depth of 6 to 8 inches. No other fertilizer elements were applied since previous experiments have demonstrated the presence of adequate amounts of phosphorous and potassium for cotton production on this soil. [1]

In 1960 nitrate nitrogen was determined from leaf petioles collected at weekly intervals from June 17 to August 26 and at biweekly

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[1] Tucker, T. C., University of Arizona. Personal communication.

intervals from August 26 to September 24. Young leaf petioles that had reached approximately full size were collected from the terminal portion of the plant. At each sampling date at least four petioles were collected from plants grown at 3 nitrogen levels at each of the 3 moisture levels. Petiole samples from six replications of each treatment were combined to give a sample of at least 24 petioles for analysis. Nitrate-nitrogen analyses were made on dried samples by a commercial laboratory (Valley Laboratories, Phoenix, Ariz.) according to methods described by Johnson and Ulrich (31).

Gibberellic Acid Treatments[2]

Gibberellic acid (GA) treatments consisted of a control (GA-0) and two formulations of GA, potassium salt (GA-1) and butyl-cellosolve ester (GA-2). These two formulations were applied July 7, July 26, and August 9 to the center two rows of 4-row plots. Applications were made with a knap-sack sprayer at the rate of 18 grams of GA in 48 gallons of water per acre. The sprayer was designed with three nozzles placed in positions to direct spray to the terminals and sides of plants (Figure 1). The nozzle tips used produced a hollow-cone spray pattern and provided complete coverage of plants so that many flower buds and bolls were treated as well as the foliage.

[2] All gibberellic acid was supplied through the courtesy of Merck and Company.

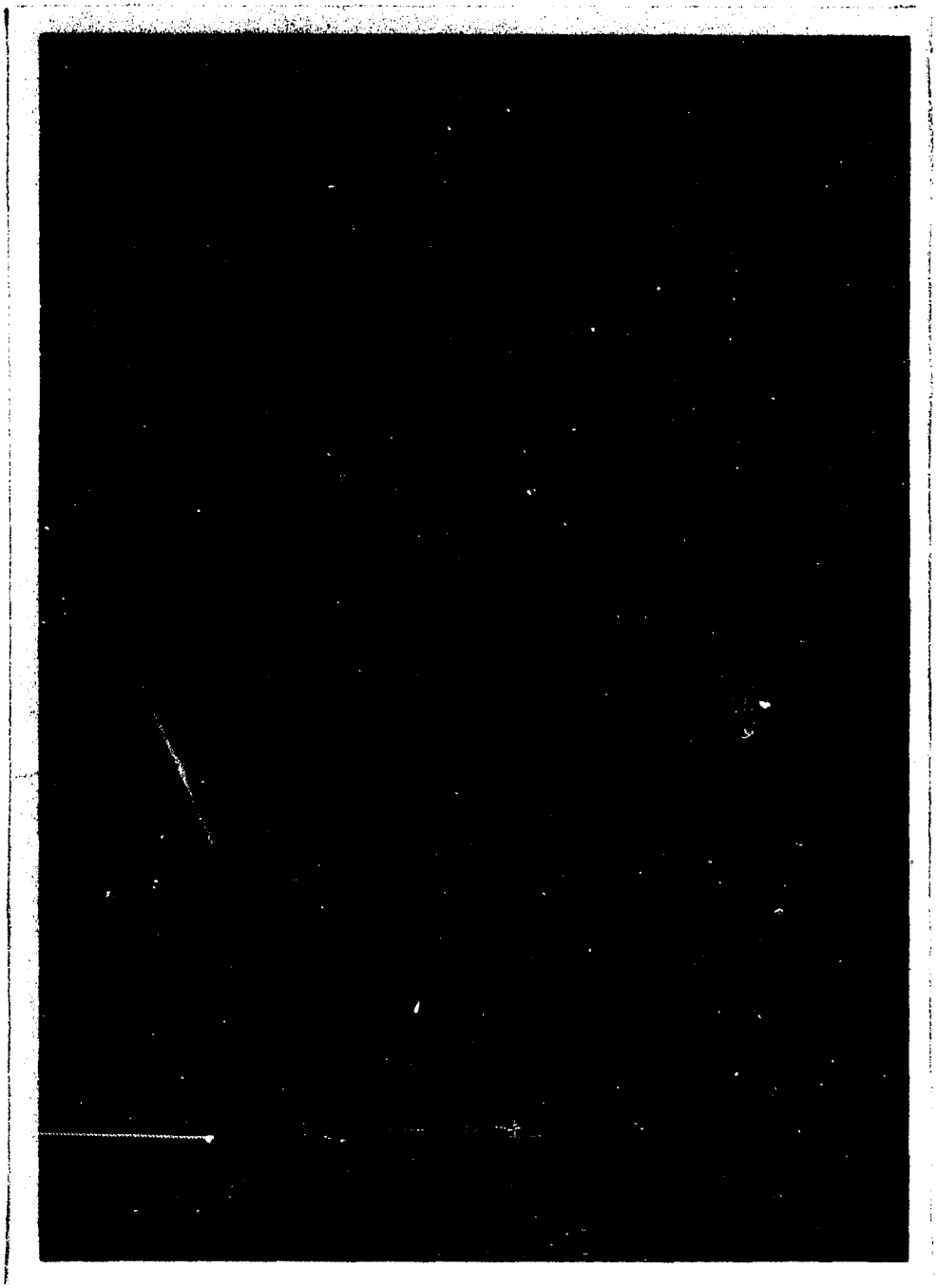


Figure 1. Spray equipment used to apply gibberellic acid to whole plants. Note the arrangement of three nozzles on the boom to direct spray to the terminals and sides of plants.

In a smaller experiment conducted in 1960, individual flowers were treated with the potassium salt of GA to further study the effect of GA on boll abscission. Open flowers were treated by spraying an aqueous solution containing 100 ppm potassium gibberellate inside the bracts with an atomizer. The spray was applied until the bracts were completely wet. Twelve plots with five plants each were selected in an area that had received 100 pounds of nitrogen at the I-M moisture level. Individual flowers in four of these plots were sprayed daily from July 10 to August 26. Flowers in four other plots were sprayed on two consecutive days at weekly intervals from July 10 to August 26. The remaining plots were used as the check. Flowering and boll abscission were studied by tagging all flowers produced daily by the method previously described.

All leaves were collected on August 3 from five plants treated daily with GA and five control plants. Dried samples were analyzed for reducing sugars and total nitrogen by methods approved by the Association of Official Agricultural Chemists (A. O. A. C.) (43). Total carbohydrates were determined indirectly by subtracting the sum of the values for ash, protein, and fat (determined by official A. O. A. C. methods) from 100 per cent. Leaf petioles were collected and analyzed for nitrate nitrogen by methods previously described. These analyses were made by Valley Laboratories, Phoenix, Arizona.

Pollination Studies

Histological methods were used to compare embryo development of abscissed and normal bolls. This was an indirect means of studying the role of nonviable pollen in boll abscission.

Normal and abscissed bolls were collected at frequent intervals from field grown plants whose flowers had been tagged daily during the growing seasons of 1959 and 1960. Abscissed bolls were collected in a turgid condition by exerting a slight pressure on many of the young bolls on a plant. This slight pressure prompted the separation of the peduncle of abscissed bolls from the fruiting branch along the abscission layer. Normal bolls of the same age were collected on the same day from adjacent plants. These bolls were selected on the basis of their apparent normal size and greener color, plus the fact that slight pressure did not dislodge them from the plant.

After bolls were collected, they were immediately immersed in formalin-acetic-alcohol (FAA). Following a killing and fixing period of not less than 48 hours, the ovules were separated from the bolls and dehydrated by the tertiary butyl alcohol series as outlined by Johansen (30). The ovules were then infiltrated and embedded in paraffin for sectioning at 15 microns with a rotary microtome. Ovules were stained with the safranin O and fast green combination (30) and counterstained with orange G.

In another experiment fresh weights of bolls at ages of 48, 72, 96, and 120 hours after anthesis were determined for bolls from both pollinated and unpollinated flowers. These weights were compared with fresh weights of bolls from pollinated flowers that abscissed at 96 and 120 hours after anthesis. Approximately 110 bolls were weighed at each period for each type of boll.

Unpollinated flowers were obtained by severing the style near the ovary with a razor blade soon after anthesis. Plants that were used to obtain pollinated and unpollinated flowers were kept free of all bolls and flowers that were not being used in the experiment. This method was used to insure that only normal bolls would be collected since Walhood (53) found that boll abscission could be reduced to a minimum by defruiting.

Auxin Determinations

The Avena curvature test, which is a standard method for the bioassay of auxin, was used in 1960 to measure auxin levels of bolls. Bolls were collected from field grown plants in an area that received 100 pounds of nitrogen at the I-M moisture level. A bioassay of auxin was made for normal bolls at ages of 48, 72, and 96 hours after anthesis, and abscissed bolls at the age of 120 hours after anthesis.

All bolls except abscissed bolls were collected from plants that were defruited. As mentioned before, this procedure was used to insure

that only normal bolls would be selected for analyses. After the bolls were collected, 10 gram samples were immediately taken to the laboratory for analyses. Each sample was immersed in 35 ml. of peroxide-free diethyl ether at 0° C. and a 24-hour extraction period was carried out in the dark at 0° C. This temperature was used to prevent enzymatic activity in the plant tissues during extraction (54).

Diethyl ether was made peroxide-free by shaking the ether in a saturated aqueous solution of ferrous sulfate that had been acidified with hydrochloric acid (29). The resulting mixture was stored at 0° C. until used. The ether was then decanted from the container for immediate use.

After the extraction period was completed, the plant material was removed, and the extract was evaporated to dryness in a water bath. The residue was redissolved in 5 ml. of ether and transferred quantitatively to a small test tube containing 0.4 ml. of 1.5 per cent molten agar. After the ether evaporated, the agar was shaken thoroughly and poured into a standard mold to form a block of dimensions 8.1 x 11.2 x 0.9 mm. In each experiment a control of 50 µg. of indole-3-acetic acid (IAA) per liter was also cast into an agar block of similar size. Each agar block was divided equally into 12 smaller blocks for use in the Avena test.

The Avena test was conducted in a chamber where temperature was controlled at 25° ± 1° C. with a relative humidity of approximately

90 per cent. Red light was used for illumination. In setting up the test, hulled seeds of Victory oats were germinated and the seedlings were transferred to Avena racks and decapitated according to the standard method described by Leopold (33). Agar blocks containing the ether extract or IAA were applied unilaterally to the cut surface of the coleoptiles. One treatment was applied to a rack of 12 Avena test plants. After the agar blocks had been on the coleoptiles for 120 minutes, shadowgraphs were made to permanently record the curvatures of the coleoptiles. An Avena protractor was then used to measure these curvatures.

Climatological Observations

Average air temperatures and total precipitation by months during the fruiting period of 1959 and 1960 are summarized in Table 1. The data were obtained from an official United States Weather Bureau recording station located at the Cotton Research Center. Temperatures were quite high throughout each season and were similar during both years. Rainfall occurred only in July and August, but the amount that fell at any period was small and did not materially alter irrigation treatments.

Table 1. Climatological observations during the fruiting period of 1959 and 1960.

Year	Average air temperatures and total precipitation, by months											
	June			July			August			September		
	max. temp.	min. temp.	total Ppt.	max. temp.	min. temp.	total Ppt.	max. temp.	min. temp.	total Ppt.	max. temp.	min. temp.	total Ppt.
	°F	°F	in.	°F	°F	in.	°F	°F	in.	°F	°F	in.
1959	106	67	0.00	107	77	0.48	100	74	1.23	97	64	0.00
1960	106	67	0.00	106	71	0.56	102	70	1.93	102	63	0.00

RESULTS AND DISCUSSION

Effects of Nitrogen and Irrigation Treatments on Plant Characteristics

Nitrate-Nitrogen Status of Treated Plants

Seasonal variations in nitrate nitrogen of petioles of plants grown at three nitrogen levels at each of three moisture levels in 1960 are presented graphically in Figures 2, 3, and 4. At each moisture level nitrate nitrogen generally decreased as the growing season advanced regardless of the amount of nitrogen applied. Such a decline could have been due to the intense demand for nitrogen by developing bolls (10). Plants grown under the N-100 and N-200 treatments maintained higher nitrate levels throughout the season than plants grown under the N-0 treatment.

A comparison of nitrate-nitrogen values for the season between the three moisture levels reveals remarkable differences. At the I-D (dry) level, (Figure 2), moisture was so limiting that uptake of nitrogen was apparently retarded except for periods following an irrigation. However, the nitrate concentration of petioles of plants remained higher over

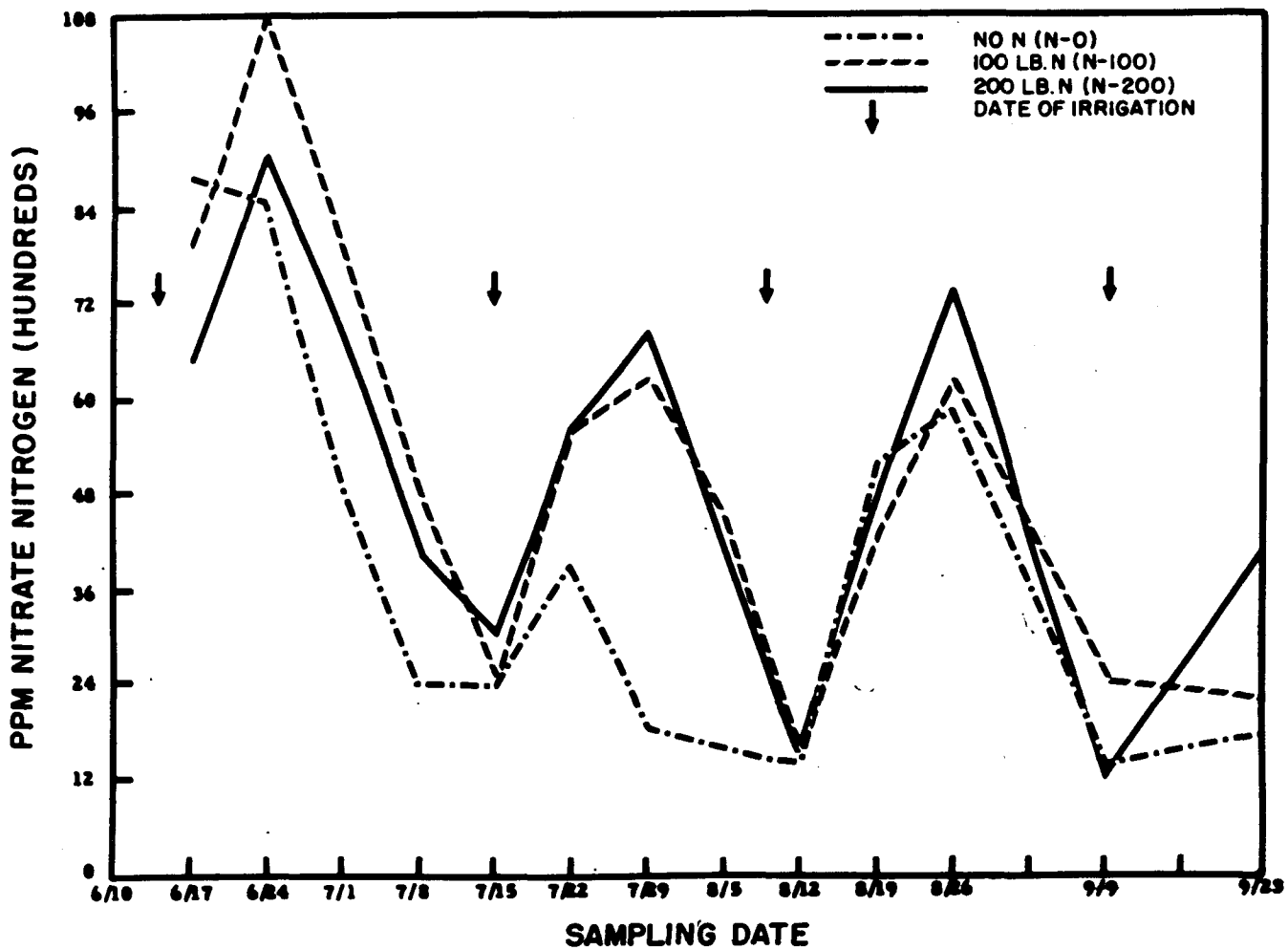


Figure 2. Seasonal trends in nitrate-nitrogen concentration of cotton petioles as affected by nitrogen at the lowest moisture level (I-D), 1960.

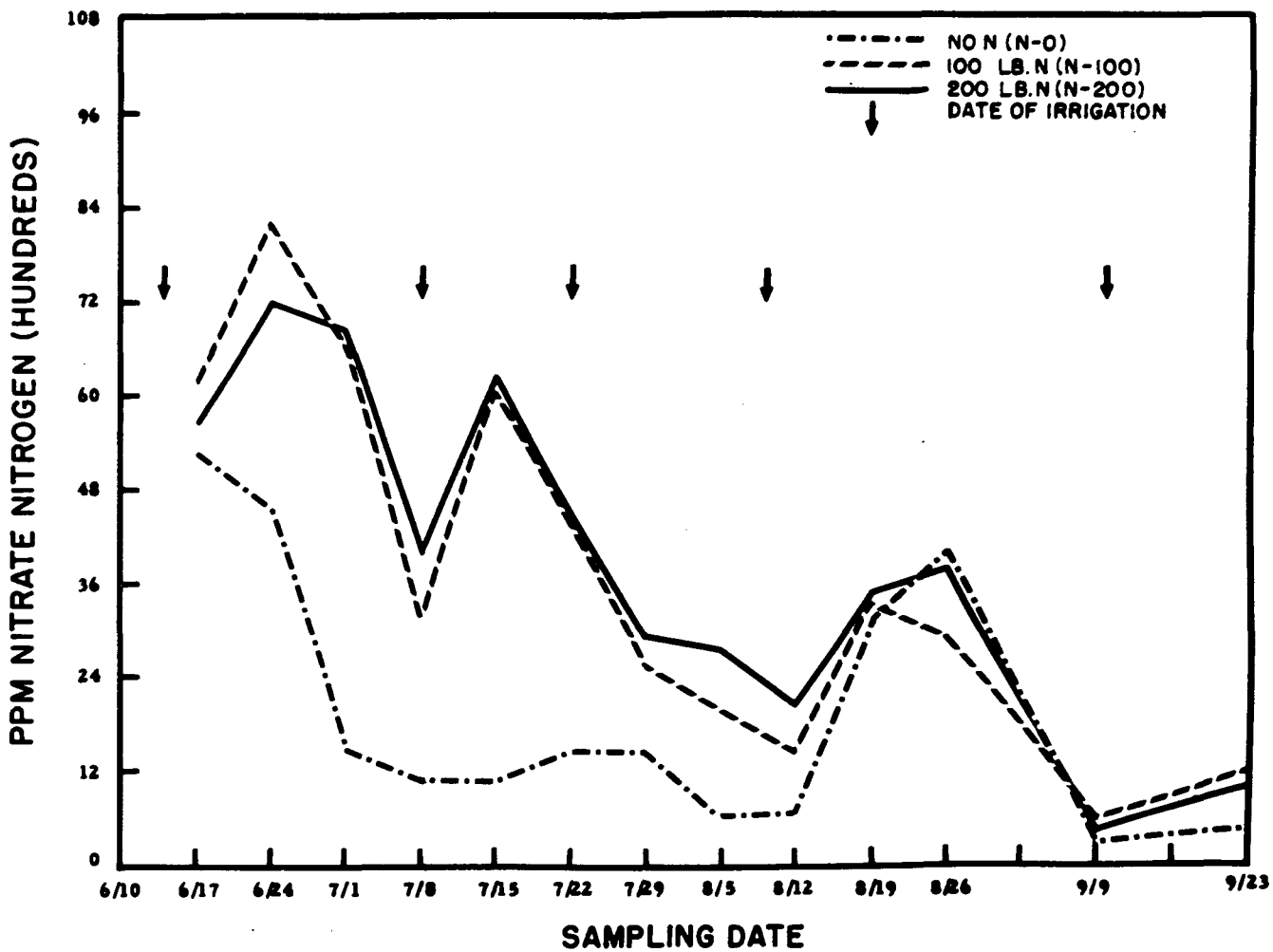


Figure 3. Seasonal trends in nitrate-nitrogen concentration of cotton petioles as affected by nitrogen at the medium moisture level (I-M), 1960.

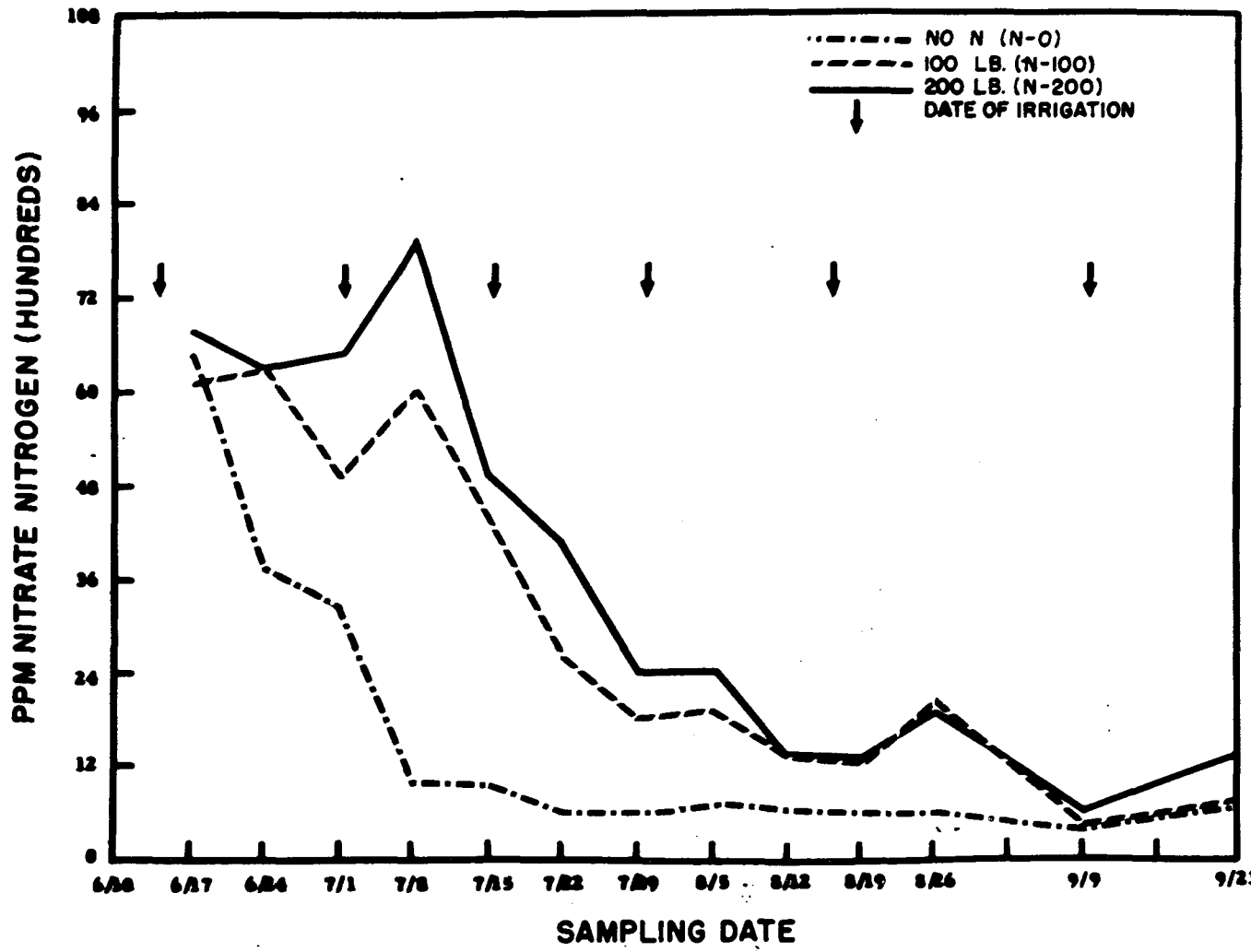


Figure 4. Seasonal trends in nitrate-nitrogen concentration of cotton petioles as affected by nitrogen at the highest moisture level (I-W), 1960.

the season than at any of the other moisture levels. The opposite extreme can be observed at the I-W (wet) level (Figure 3) where frequent irrigations caused a more rapid decline in nitrate-nitrogen concentrations, probably due to more leaching of nitrogen and a more rapid rate of plant growth. Nitrate-nitrogen levels for the I-M (medium) treatment (Figure 4) were intermediate between these two extremes.

The rapid rise in nitrate-nitrogen concentration at practically all treatments during the period from August 12 to August 26 was probably due to the maturation of bolls that formed early in the season. Thus, more nitrogen was made available for new vegetative growth. The abrupt increase in flowering that occurred during the latter portion of this period (Figures 5 and 6) also confirms the proposal that increased nitrate-nitrogen concentration in the plant was associated with renewed growth.

Flowering and Growth Relationships

Since cotton has an indeterminate growth habit and produces flowers at most nodes of fruiting branches, a study of flower production is an excellent means of studying the over-all growth of the cotton plant. However, since floral buds are initiated approximately 30 days before anthesis, no direct relationship exists between flowering and

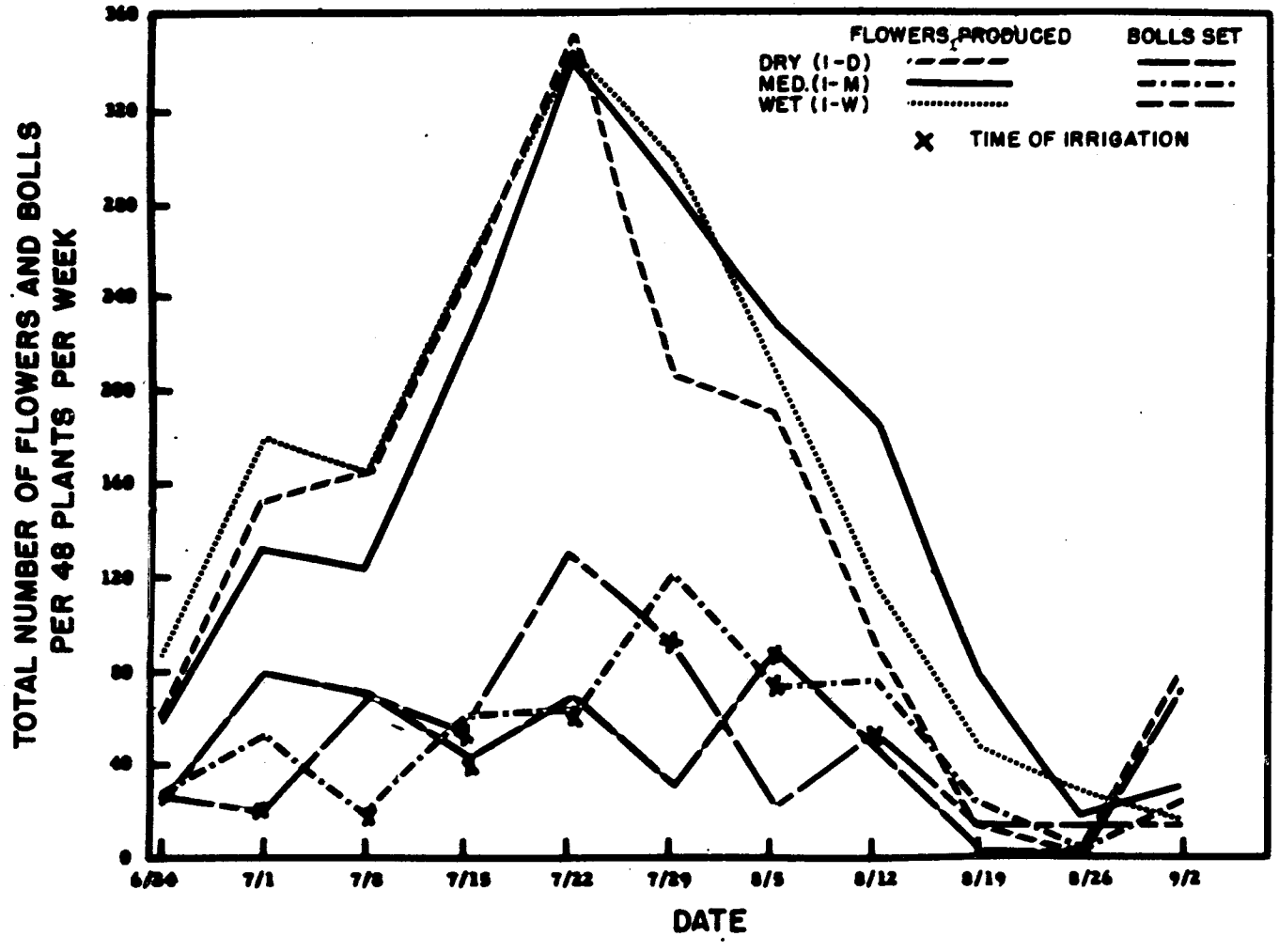


Figure 5. Seasonal trend in fruiting behavior as affected by moisture, 1960.

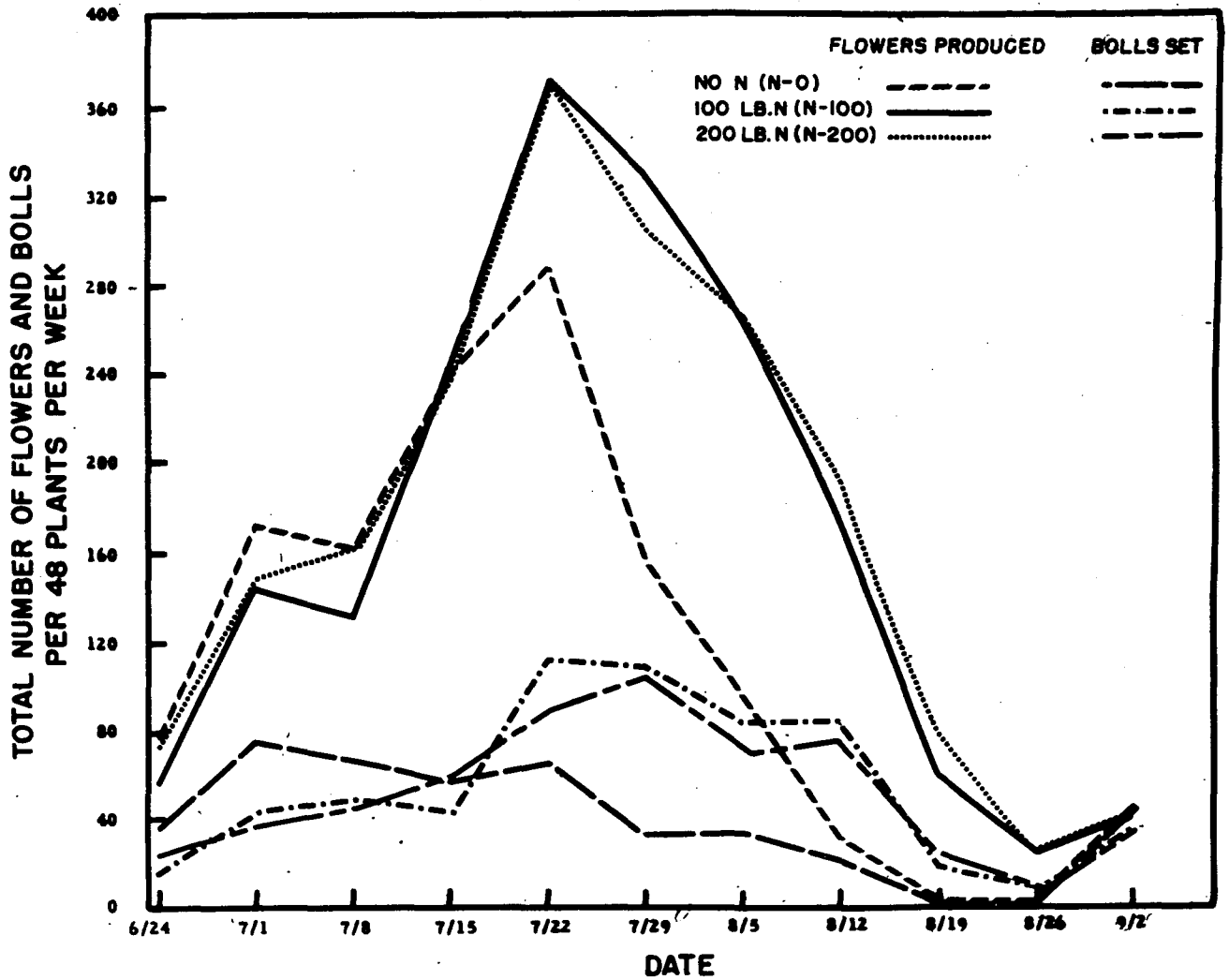


Figure 6. Seasonal trend in fruiting behavior as affected by nitrogen, 1960.

treatment for any particular period. Flowering relationships for moisture and nitrogen treatments may be followed in Figures 5 and 6 and Tables 2 and 3. Individual plants grown in 1959 produced more flowers than plants grown in 1960. This relationship was probably due to the closer spacing of plants grown in 1960.

Moisture stress (I-D treatment) resulted in a much greater reduction in flowering as the season progressed during 1959 than in 1960 (Tables 2 and 3). However, plants grown at the I-D treatment in 1960 received one more irrigation early in the season than plants grown under this treatment in 1959. Such a reduction in flowering emphasizes the importance of an adequate moisture supply early in the season when meristematic growth is very rapid. There was a tendency for greater flower production at the I-W moisture level than at the I-M level during the period from June 20 to August 1 (Tables 2 and 3). However, flower production was lower during September at the I-W level so there was very little difference between the two treatments for the entire season. Decreased flower production during September at the I-W treatment may have been due to the low nitrate-nitrogen status of plants (Figure 4).

A nitrogen deficiency (N-0 treatment) resulted in extreme retardation of growth and thus less flowering during both years (Tables 2 and 3). However, the N-100 and N-200 treatments reacted similarly during both 1959 and 1960, indicating that factors other than nitrogen were limiting

Table 2. Flowering periodicity as affected by moisture and nitrogen, 1959.

Treatment	Average number of flowers produced per four plants, by periods			
	6/20-7/31	8/1-8/31	9/1-9/23	Total
Moisture				
Dry (I-D)	128	47	22	197
Medium (I-M)	151	105	48	305
Wet (I-W)	186	91	20	297
Nitrogen				
No N (N-0)	149	55	24	228
100 lb. N/acre (N-100)	155	103	36	294
200 lb. N/acre (N-200)	161	85	30	277
L. S. D. --5% level (N treatments)	N. S.	21	N. S.	37

Table 3, Flowering periodicity as affected by moisture and nitrogen, 1960. [1]

Treatment	Average number of flowers produced per four plants, by periods			
	6/20-7/31	8/1-8/31	9/1-9/10	Total
Moisture				
Dry (I-D)	93	41	8	141
Medium (I-M)	85	53	4	142
Wet (I-W)	91	55	2	148
Nitrogen				
No N (N-0)	80	23	4	107
100 lb. N/acre (N-100)	92	62	5	159
200 lb. N/acre (N-200)	97	63	5	165
L. S. D. --5% level (N treatments)	10	7	N. S.	16

[1] Data taken from larger experiment with irrigation treatments as whole plots, nitrogen treatments as subplots, and gibberellic acid treatments as sub-subplots.

flower production. Nitrogen and moisture treatments were evidently acting independently since no interaction was found for these two factors.

The peak for flowering occurred during the period from July 22 to 29 for all moisture and nitrogen treatments in 1960 (Figures 5 and 6). A similar growth pattern was observed in 1959 (not presented). Therefore, one may assume that rate of growth in terms of rapid cell division at shoot apices also reached its peak approximately 30 days earlier when the corresponding floral buds were initiated. This peak thus occurred during the latter part of June and decreased, as flowering did, at a fairly rapid rate thereafter.

Moisture and nitrogen treatments in 1960 affected growth in height in a manner similar to that found for flowering (Table 4). Plants receiving nitrogen grew taller than plants grown at a deficient nitrogen level. The effect of moisture stress on plant height was not as pronounced as the nitrogen effect.

Boll Abscission and Fruiting Relationships

The preceding results showed that nitrogen and irrigation treatments were successful in altering growth and the nitrate-nitrogen status of cotton plants. These conditions were created primarily to provide a basic experiment for a study of boll abscission.

Table 4. Height of cotton plants as affected by moisture and nitrogen, 1960.[1]

Treatment	Average height per plant	
	7/13	8/24
	(inches)	(inches)
Moisture		
Dry (I-D)	26.7	37.8
Medium (I-M)	26.7	40.8
Wet (I-W)	30.0	42.2
Nitrogen		
No N (N-0)	25.8	34.4
100 lb. N/acre (N-100)	28.5	42.7
200 lb. N/acre (N-200)	29.0	43.8
L.S.D. --5% level (N treatments)	0.7	1.7

[1] Data taken from larger experiment with irrigation treatments as whole plots, nitrogen treatments as subplots, and gibberellic acid treatments as sub-subplots.

The influences of moisture and nitrogen treatments on boll abscission are presented in Tables 5 and 6 for 1959 and 1960, respectively. All values are presented as the percentage of bolls that abscissed. The consistently high values for all treatments have been observed by other workers (4, 24, 49); however, two basic trends seem to be evident. First, percentage boll abscission was decreased by the N-0 treatment at all periods (significantly so only in 1960), and second, percentage boll abscission decreased as the growing season progressed. The results in the preceding section showed that vegetative growth in terms of flowering was decreased by a nitrogen deficiency (Tables 2 and 3). Rate of growth in terms of flowering also decreased as the season advanced. One may logically assume, then, that increased vegetative growth was responsible in some degree for increased boll abscission. Competition for available nutrients between vegetative growing points and developing bolls could have been the primary cause of increased boll abscission.

The effects of moisture treatments on percentage boll abscission were not well-defined (Tables 5 and 6). However, percentage boll abscission was less under the I-W treatment during the period from June 20 to August 1 during both 1959 and 1960. This decrease was then compensated for during the following period in August, since percentage boll abscission was higher than that observed for the other moisture treatments. Such a relationship is difficult to explain in terms of

Table 5. Percentage boll abscission as affected by moisture and nitrogen, 1959.

Treatment	Average percentage abscission per four plants, by periods		
	6/20-7/31	8/1-8/31	Season (6/20-9/23)
Moisture			
Dry (I-D)	71.9	61.0	64.5
Medium (I-M)	76.4	60.3	66.2
Wet (I-W)	70.0	66.9	66.2
Nitrogen			
No N (N-0)	70.9	60.4	64.0
100 lb. N/acre (N-100)	73.6	65.5	66.6
200 lb. N/acre (N-200)	73.9	62.2	66.3
L. S. D. --5% level (N treatments)	N. S.	N. S.	N. S.
Average per period	72.8	62.7	
	L. S. D. (5% level) = 5.3		

Table 6. Percentage boll abscission as affected by moisture and nitrogen, 1960. [1]

Treatment	Average percentage abscission per four plants, by periods		
	6/20-7/31	8/1-8/31	Season (6/20-9/10)
Moisture			
Dry (I-D)	69.7	56.3	62.3
Medium (I-M)	71.8	55.6	65.0
Wet (I-W)	65.6	71.8	67.4
Nitrogen			
No N (N-0)	65.4	56.9	61.4
100 lb. N/acre (N-100)	70.6	62.3	65.8
200 lb. N/acre (N-200)	71.2	64.5	67.4
L. S. D. --5% level (N treatments)	2.4	5.7	2.0
Average per period	69.0	61.2	
	L. S. D. (5% level) = 2.6		

[1] Data taken from larger experiment with irrigation treatments as whole plots, nitrogen treatments as subplots, and gibberellic acid treatments as sub-subplots.

available moisture since there was no systematic relationship from the lowest to the highest moisture level at either period.

The actual number of bolls that set at different periods during 1959 and 1960 are presented in Tables 7 and 8, respectively. The number of bolls that set is directly dependent on the number of flowers and percentage boll abscission. Since percentage abscission did not vary greatly between treatments, trends for boll set generally follow trends that were evident for flowering (Tables 2 and 3).

When moisture or nitrogen were not limiting,the peak for the number of bolls that set corresponded closely to the peak for the number of flowers produced (Figures 5 and 6). Such a relationship would be expected if boll abscission percentages were somewhat uniform throughout the season and unaffected by moisture or nitrogen deficiencies. A delay in the peak for bolls that set under the I-D treatment was undoubtedly due to the low moisture level during the time preceding this peak (Figure 5). Plants grown under the nitrogen deficient level set more bolls early in the season, but the number of bolls that set thereafter declined rapidly (Figure 6).

The immediate effect of an irrigation on boll set may be followed graphically in Figure 7. One may assume that any immediate effect would be expressed by an increase in the number of bolls that set during a period from one or two days before an irrigation to one or two days

Table 7. Effects of moisture and nitrogen on the number of bolls set (matured), 1959.

Treatment	Average number of bolls set per four plants, by periods			
	6/20-7/31	8/1-8/31	9/1-9/23	Total
Moisture				
Dry (I-D)	37	17	16	69
Medium (I-M)	36	41	27	103
Wet (I-W)	56	29	15	99
Nitrogen				
No N (N-0)	44	21	17	82
100 lb. N/acre (N-100)	41	35	21	97
200 lb. N/acre (N-200)	43	30	19	92
L. S. D. --5% level (N treatments)	N. S.	8	N. S.	6

Table 8. Effects of moisture and nitrogen on the number of bolls set (matured), 1960. [1]

Treatment	Average number of bolls set per four plants, by periods			
	6/20-7/31	8/1-8/31	9/1-9/10	Total
Moisture				
Dry (I-D)	28	18	7	53
Medium (I-M)	24	22	3	48
Wet (I-W)	31	15	2	48
Nitrogen				
No N (N-0)	28	9	4	41
100 lb. N/acre (N-100)	27	23	4	54
200 lb. N/acre (N-200)	28	22	4	54
L. S. D. --5% level (N treatments)	N. S.	3	N. S.	6

[1] Data taken from larger experiment with irrigation treatments as whole plots, nitrogen treatments as subplots, and gibberellic acid treatments as sub-subplots.

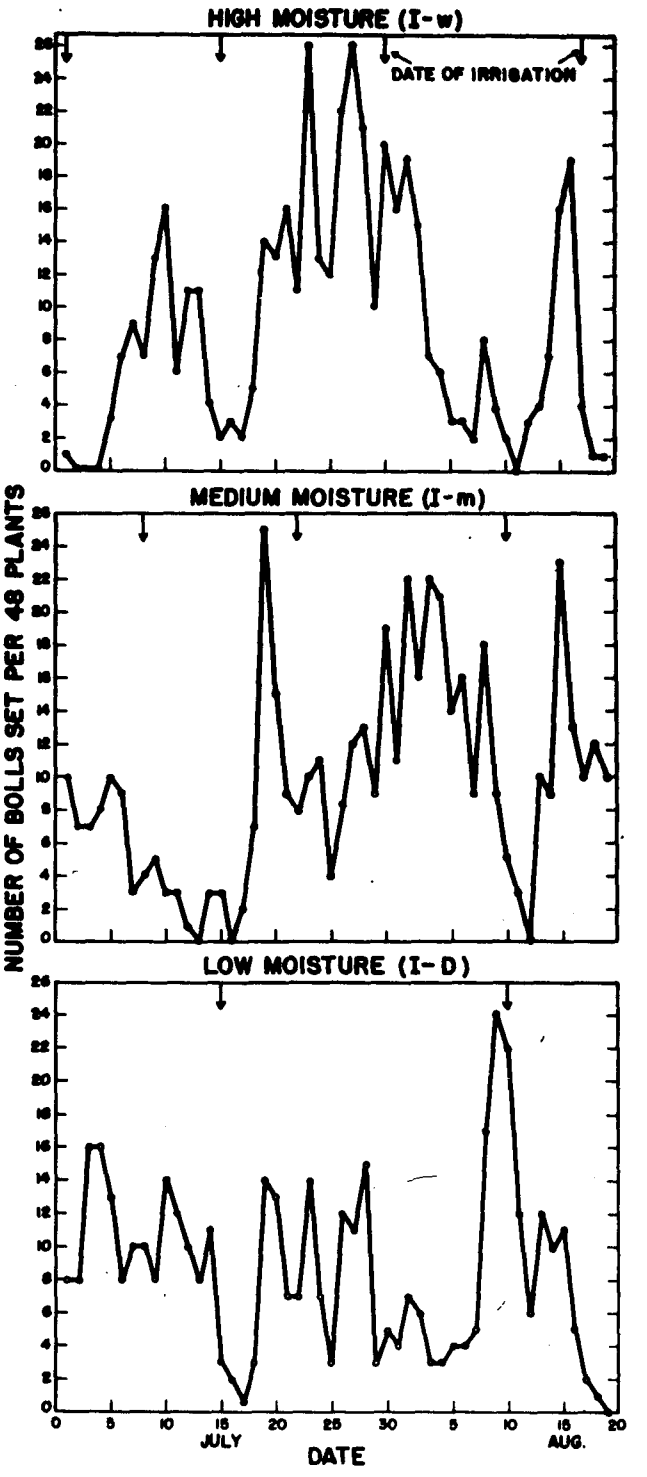


Figure 7. Number of bolls set daily on cotton plants grown under three moisture levels. July 1 to August 19, 1960.

after. Such an effect was not evident under any of the moisture treatments, except for the irrigation that occurred on August 10 at the lowest moisture level (I-D treatment). As previously mentioned, decreased moisture tension after an irrigation at the I-D moisture level was also accompanied by a pronounced increase in the nitrate-nitrogen concentration in the plants (Figure 2). Thus, the observed increase in the number of bolls that set could have been more directly influenced by an increase in available nitrogen. The failure of a similar response for the irrigation that occurred on July 15 at the I-D level may have been the result of the existing boll load and any renewed growth that followed this irrigation.

Nitrate-nitrogen Status of Plants and Fruiting Relationships

Since nitrate-nitrogen concentrations of plants were altered by nitrogen treatments (Figures 2, 3, and 4), values for nitrate-nitrogen concentrations and fruiting properties during the growing season of 1960 are presented in Table 9 for detailed study. Correlations were determined for many of the factors that were compared at weekly intervals from June 24 until flowering "cut-out" approached on August 19 (Table 10).

Nitrate nitrogen was negatively correlated with accumulated bolls (boll load) at all nitrogen levels (Table 10). Such a relationship suggests

Table 9. Effects of nitrogen on nitrate-nitrogen levels of petioles and fruiting properties of cotton plants, 1960.[1]

Weekly Period	Average nitrate N concentration			Fruiting properties per four plants											
				Percentage abscission			Bolls assumulated (boll load)			Bolls set (matured)			Flowers produced		
	Lb. N/acre			Lb. N/acre			Lb. N/acre			Lb. N/acre			Lb. N/acre		
	0	100	200	0	100	200	0	100	200	0	100	200	0	100	200
	ppm in hundreds			per cent			number			number			number		
6/24 - 6/30	44	75	71	52.6	71.5	66.7	3.0	1.3	2.0	3.0	1.3	2.0	6.3	4.7	6.0
7/1 - 7/7	24	56	60	56.1	70.6	76.3	9.3	4.9	4.9	6.3	3.6	2.9	14.3	12.2	12.3
7/8 - 7/14	15	45	50	58.9	63.9	72.2	14.8	8.9	8.7	5.6	4.0	3.8	13.6	11.1	13.5
7/15 - 7/21	18	43	47	76.3	82.5	75.1	19.6	12.5	13.6	4.8	3.6	4.9	20.0	20.5	19.8
7/22 - 7/28	11	39	44	77.0	70.1	76.5	25.1	21.8	20.9	5.5	9.3	7.3	23.9	31.3	31.3
7/29 - 8/4	12	32	37	79.7	67.0	66.4	27.8	30.1	29.5	2.7	9.1	8.6	13.2	27.5	25.5
8/5 - 8/11	10	22	25	65.3	68.8	74.5	30.5	37.8	35.2	2.8	6.9	5.7	7.9	22.2	22.3
8/12 - 8/18	20	23	25	32.2	52.0	61.4	32.3	44.7	41.3	1.8	6.9	6.2	2.6	14.4	16.0
8/19 - 8/25	33	34	39	--	70.5	69.6	0.0	46.2	43.3	0.0	1.5	2.0	0.0	5.1	6.6
8/26 - 9/1	--	--	--	--	67.8	66.5	0.0	46.9	44.0	0.0	0.7	0.7	0.0	2.1	2.0
9/2 - 9/8	7	11	8	9.3	12.3	14.6	35.6	49.8	46.9	3.3	2.9	2.9	3.7	3.3	3.4
Total				66.3	67.7	70.4				35.6	49.8	46.9	105.4	154.3	158.6

[1] Averages of 3 irrigation levels.

Table 10. Correlations of fruiting properties with nitrate-nitrogen concentrations compared at weekly intervals for three nitrogen levels from June 24 to August 19, 1960.

Fruiting properties	Nitrate-nitrogen concentrations			Percentage abscission		
	Lb. N/acre			Lb. N/acre		
	0	100	200	0	100	200
	Correlation coefficient					
Percentage abscission	-0.671*	+0.436	+0.213	---	---	---
Bolls accumulated (boll load)	-0.781*	-0.915*	-0.961*	+0.773*	-0.598	-0.400
Boll set	-0.223	-0.803*	-0.740*	---	---	---

* Significant at 5% level.

that developing bolls were a major user of available nitrogen in the plant.

Correlations that exist between nitrate nitrogen and bolls that set at weekly intervals are of particular interest since the number of bolls retained at any particular period is directly dependent on the nutritional status of the plant for that period. Plants grown at the N-100 and N-200 levels retained more bolls as nitrate nitrogen decreased (Table 10). This relationship could have been due to the dominating effect of growth which was rapid early in the season when nitrate concentrations were high. Such an assumption may also explain the lack of a correlation for plants grown at the N-0 level, since nitrate concentrations were considerably less at this treatment (Table 9).

Percentage abscission was correlated with both nitrate-nitrogen concentration and accumulated bolls (boll load) at the N-0 treatment level (Table 10). Percentage abscission increased as nitrate nitrogen decreased and increased as boll load increased. Since increased boll load was also associated with decreased nitrate concentration, these two correlations complement each other.

The validity of comparing percentage abscission with the nitrate-nitrogen status of plants is somewhat questionable. Since percentage abscission is dependent on two factors (flowering and boll set) that are initiated 30 days apart, nutritional conditions which may be quite

favorable for floral bud initiation may change within a 30-day period to be unfavorable for boll set. Thus, as mentioned before, the actual number of bolls that set within a particular period is probably a better criterion to compare with the nitrogen status of plants.

Yield Relationships

A comparison of yields during the growing seasons of 1959 and 1960 (Tables 11 and 12, respectively) shows many similar responses to moisture and nitrogen treatments, but two primary differences are also apparent. First, total yields for the I-D treatment were of a much greater magnitude in 1960 than in 1959. As previously mentioned, this was probably the result of increased growth due to one more irrigation early in the season in 1960. Second, total yields were significantly increased over all nitrogen treatments by the N-200 treatment in 1960, while in 1959 no significant difference was found between the N-100 and N-200 treatments. Significant interactions between moisture and nitrogen treatments that have been observed by other workers (23, 45) were not found in either of these experiments.

The characteristic trend for heavier fruiting during June and July by the I-W treatment that was reported in previous sections was again evident at the first date of picking during both 1959 and 1960 (Tables 11 and 12). No explanation is given for this relationship. The

Table 11. Calculated yields of lint cotton per acre as affected by moisture and nitrogen, 1959.

Treatment	Date of picking			
	9/22	11/9	1/7/60	Total
	lbs.	lbs.	lbs.	lbs.
Moisture				
Dry (I-D)	467	240	183	890
Medium (I-M)	524	530	355	1,409
Wet (I-W)	739	319	238	1,296
Nitrogen				
No N (N-0)	615	272	223	1,110
100 lb. N (N-100)	567	407	272	1,246
200 lb. N (N-200)	548	410	281	1,240
L. S. D. --5% level (N treatments)	50	43	35	43

Table 12. Calculated yields of lint cotton per acre as affected by moisture and nitrogen, 1960. [1]

Treatment	Date of picking			
	9/26	11/5	12/16	Total
	lbs.	lbs.	lbs.	lbs.
Moisture				
Dry (I-D)	570	286	431	1,287
Medium (I-M)	715	426	202	1,342
Wet (I-W)	818	289	96	1,204
Nitrogen				
No N (N-0)	654	210	283	1,146
100 lb. N (N-100)	699	380	211	1,289
200 lb. N (N-200)	750	412	236	1,398
L. S. D. --5% level (N treatments)	58	52	46	52

[1] Data taken from larger experiment with irrigation treatments as whole plots, nitrogen treatments as subplots, and gibberellic acid treatments as sub-subplots.

low yield for this treatment at the last date of picking was probably due to the low nitrate-nitrogen status of these plants during August (Figure 4) which prevented renewed growth and flowering in September.

Yields of lint cotton are dependent on the number of bolls that set, boll size (bolls per pound), and lint percentage. Yields in 1959 closely followed trends that were found for the number of bolls that set (Table 7). This was true since boll size and lint percentage (Tables 23 and 27, respectively) were relatively unaffected by treatments, with the exception of a reduction in boll size at the I-D treatment. In 1960, however, the number of bolls that set (Table 8) was a poor indicator of actual yield. Even though the I-D treatment increased the number of bolls that set in 1960, yields did not follow this trend probably due to decreased boll size (Table 24). Such a reduction in boll size was probably due to periods of extreme stress for water and nitrogen which prevented normal growth of bolls. The fact that more small bolls were retained on plants grown under this treatment indicates that plants were able to compensate for decreased boll size during periods of adequate moisture.

There was no significant difference in the number of bolls that set between the N-100 and N-200 treatments in 1960 (Table 8), but there was a significant increase in yield due to the N-200 treatment. Increased

boll size for the N-200 treatment (Table 24)was apparently responsible for this relationship.

Effects of Gibberellic Acid Treatments on Plant Characteristics

Treatment of Whole Plants

Growth and Fruiting Relationships. Spraying of whole plants with two formulations of gibberellic acid (GA-1 and GA-2) in 1960 resulted both in increased growth in height (Table 13) and production of more flowers for the growing season (Table 14). Increased flower production may have been the result of either an increased rate of growth, or an increased retention of floral buds, or both. No significant differences were observed between the effects of either formulation of GA.

Immediate effects of GA treatments on percentage boll abscission were determined from flowers that were at anthesis during a period ranging from two days before to two days after the day of treatment. These effects, at each of three treatment dates, are shown in Table 15. Over-all effects for different periods during the growing season are presented in Table 14.

No significant decrease in percentage boll abscission was observed for the immediate effect of GA at either of the two treatment dates in July (Table 15). However, there were trends to this effect at

Table 13. Growth in height of cotton plants as affected by spraying whole plants with two formulations of gibberellic acid on July 7, July 26, and August 9, 1960. [1]

Treatment	Average growth per plant from 7/13 to 8/24	Average height per plant on 8/24
	inches	inches
Control (GA-0)	11.3	38.5
Potassium salt of GA (GA-1)	12.9	41.0
Butyl-cellosolve ester of GA (GA-2)	13.4	41.4
L.S.D. --5% level	0.6	0.7

[1] Data taken from larger experiment with irrigation treatments as whole plots, nitrogen treatments as subplots, and gibberellic acid treatments as sub-subplots.

Table 14. Fruiting characteristics during the growing season as affected by spraying whole plants with two formulations of gibberellic acid on July 7, July 26, and August 9, 1960. [1]

Treatment	Averages per four plants, by periods			
	6/20-7/31	8/1-8/31	9/1-9/10	Total
	Number of flowers produced			
Control (GA-0)	86.9	45.6	3.6	136.1
Potassium salt of GA (GA-1)	92.6	50.4	5.3	148.2
Butyl-cellosolve ester of GA (GA-2)	88.9	52.7	5.2	146.7
L.S.D. --5% level	N.S.	N.S.	N.S.	8.9
	Number of bolls set			
Control (GA-0)	25.3	15.7	3.1	44.1
Potassium salt of GA (GA-1)	29.7	19.2	4.7	53.6
Butyl-cellosolve ester of GA (GA-2)	27.3	19.6	4.2	51.1
L.S.D. --5% level	1.5	N.S.	N.S.	3.8
	Percentage boll abscission			
Control (GA-0)	70.9	62.8	--	67.2
Potassium salt of GA (GA-1)	67.4	60.3	--	63.2
Butyl-cellosolve ester of GA (GA-2)	68.9	60.6	--	64.3
L.S.D. --5% level	1.9	N.S.	--	1.9

[1] Data taken from larger experiment with irrigation treatments as whole plots, nitrogen treatments as subplots, and gibberellic acid treatments as sub-subplots.

Table 15. Effect of gibberellic acid treatments (whole-plant applications) on percentage boll abscission of flowers that were at anthesis during a period ranging from 2 days before to 2 days after the day of treatment, 1960.[1,2]

Treatment	Average percentage abscission per four plants, by periods		
	7/5-7/9	7/24-7/28	8/7-8/11
	pct.	pct.	pct.
Control (GA-0)	67.6	75.4	67.6
Potassium salt of GA (GA-1)	61.0	69.6	50.8
Butyl-cellosolve ester of GA (GA-2)	62.3	73.4	46.7
L.S.D.--5% level	N.S.	N.S.	9.2

[1] GA treatments applied July 7, July 26, and August 9.

[2] Data taken from larger experiment with irrigation treatments as whole plots, nitrogen treatments as subplots, and gibberellic acid treatments as sub-subplots.

these treatment dates, and a significant decrease was found when the over-all period from June 20 to August 1 was considered (Table 14). Gibberellic acid treatments in August resulted in an immediate decrease in percentage boll abscission (Table 15). However, this decrease was evidently followed by an increase in percentage abscission since there was no significant difference for the over-all period for August (Table 14). A greater immediate response to GA treatments in August probably was more than an incidental relationship since, as observed before, there is a natural tendency for less percentage abscission as the season progresses. This relationship may have been due to a decline in the dominating effect of vegetative growth during the latter part of the growing season. Even though responses to GA were erratic from one period of treatment to another, all treatments as a whole were quite effective since approximately 19 per cent more bolls were set for the season when GA was used (Table 14). Both formulations of GA were equally effective in altering fruiting characteristics.

One should recall that GA treatments were a part of a larger experiment which also included moisture and nitrogen variables. However, no interactions were found between the effects of GA and the effects of moisture or nitrogen.

Previous experiments have shown that percentage boll abscission can be greatly reduced by treating individual bolls with GA (51, 53).

Thus, one may assume that the stimulus that initiates boll abscission is produced by the boll involved. The role of GA in the abscission process is unknown, but it may be associated in some way with increased auxin production. In this experiment a decrease in percentage abscission could have been due either to direct treatment of flowers and young bolls when plants were sprayed with GA, or to translocation of GA from leaves to flowers and young bolls.

Yield Relationships. Yield of lint cotton was not significantly increased by GA treatments (Table 16) even though such treatments increased the number of bolls that set (Table 14). The striking decrease in boll size (Table 24) that was associated with GA treatments undoubtedly prevented increased yields. Reduced boll size was not entirely due to increased boll load, however, since the increased vegetative growth that occurred might have been capable of causing a reduction in boll size (53).

One must be impressed by the delicate balance which exists in the cotton plant to cause such an adjustment in boll size as a result of comparatively small increases in vegetative growth and boll load. Such a phenomenon suggests that the nutritional status of the plant becomes the limiting factor for increased yields. High rates of nitrogen (N-200 treatment) were not effective in altering any of the trends associated with GA treatments (no significant interactions). Thus, it must be

Table 16. Calculated yields of lint cotton per acre as affected by spraying whole plants with two formulations of gibberellic acid on July 7, July 26, and August 9, 1960.[1]

Treatment	Date of picking			
	9/26	11/5	12/16	Total
	lbs.	lbs.	lbs.	lbs.
Control (GA-0)	692	345	244	1,280
Potassium salt of GA (GA-1)	721	328	249	1,298
Butyl-cellosolve ester of GA (GA-2)	690	328	237	1,255
L. S. D. --5% level	N. S.	N. S.	N. S.	N. S.

[1] Data taken from larger experiment with irrigation treatments as whole plots, nitrogen treatments as subplots, and gibberellic acid treatments as sub-subplots.

assumed that nitrogen was either not limiting or nitrogen uptake was actually retarded by increased boll load, as others have proposed (10, 49).

Treatment of Individual Flowers

Fruiting Relationships. When individual flowers were sprayed with GA at daily and weekly intervals, percentage boll abscission was decreased and the number of bolls that set was increased (Table 17). However, the increased boll load that resulted from these treatments caused substantial reductions in boll size (Table 17). Such reductions were especially pronounced for bolls from flowers that were treated daily since approximately 30 more bolls were required to make a pound of seed cotton. Such an adverse effect was much less for the flowers treated weekly since plants were apparently able to compensate for increased boll load by causing a greater percentage abscission during succeeding periods. This was shown by the fact that 79 per cent of the bolls from untreated flowers were abscissed compared to 67 per cent for the control (Table 17).

Nutritional Relationships. There has been much speculation concerning the relationship between the nutritional status of the cotton plant and boll abscission. Although several experiments have been designed to study these relationships, no particular nutrient has ever been directly associated with the boll abscission phenomenon. Such

Table 17. Fruiting characteristics during the growing season as affected by spraying individual flowers with gibberellic acid at daily and weekly intervals from July 10 to August 24, 1960.

Treatment	Averages per plant, by periods		
	7/10-7/31	8/1-8/23	Total
	Number of flowers produced		
Control	18.1	19.6	37.8
Sprayed weekly	20.2	18.9	39.1
Sprayed daily	19.5	12.8	32.3
	Number of bolls set		
Control	4.5	7.8	12.3
Sprayed weekly	6.2	9.1	15.3
Sprayed daily	11.5	8.9	20.4
	Percentage boll abscission		
Control	75.2	60.5	67.6
Sprayed weekly			
(a) Total flowers	69.3	51.9	60.9
(b) Untreated flowers	84.3	72.7	79.0
(c) Treated flowers	30.4	14.7	21.8
Sprayed daily	40.9	30.9	36.9
	Number of bolls per lb.		
Control	76.5	74.3	75.4
Sprayed weekly	83.3	86.0	84.7
Sprayed daily	109.7	107.0	108.3

studies have been hindered since the boll abscission process undoubtedly acts as a "safety valve" to prevent a nutritional deficiency and thus smaller bolls which would result from an excessive boll load. Thus, any nutrient or nutrients that are actually limiting for boll production never become apparent. The present study offered an excellent opportunity to study the nutritional status of the plant when a heavier than normal boll load was induced by the use of GA treatments.

Plants whose flowers had been treated daily with GA-1 were used for chemical analyses. When leaves and petioles were collected on August 3, these plants were 10 inches shorter, but contained approximately 2 1/2 times more bolls than the control (Figure 8).

Nitrogen was obviously depleted from both leaves and petioles of plants treated with GA (Table 18). Since these plants were grown in an area that received 100 pounds of nitrogen per acre, the concentration of nitrogen in the soil probably had no influence on this relationship. Therefore, one must assume that the utilization of nitrogen due to demands of a heavy boll load was far in excess of the actual rate of absorption.

Reducing sugars (glucose and fructose) which are the main sugars of cotton leaves (40) were also reduced to some extent by GA treatments (Table 18). However, total carbohydrates which include such reserve carbohydrates as starch were not reduced (Table 18). If

Figure 8. Typical cotton plants showing effects of gibberellic acid treatment. Plant on left was untreated. Flowers produced on the plant on the right were treated on the day of anthesis with 100 ppm gibberellic acid. Note the heavier boll load and smaller size of the treated plant.

Table 18. Composition of cotton leaves and petioles as affected by spraying individual flowers with gibberellic acid at daily intervals from July 10 to August 3, 1960.[1]

Plant part	Nitrate-nitrogen	Total nitrogen	Total carbohydrate	Reducing sugar[2]
	ppm	pct.	pct.	pct.
Leaves				
(a) Control	735	3.59	47.93	2.73
(b) Treated	588	3.16	48.36	2.53
Petioles				
(a) Control	4,410	---	---	---
(b) Treated	2,499	---	---	---

[1] Results reported on oven dry basis.

[2] Expressed as invert sugar.

nitrogen was not limited in the plant, one would expect a depletion of carbohydrates due to increased respiration and increased assimilation of nitrogen which would be required by an unusually heavy boll load. The fact that total carbohydrates were not reduced would again indicate that a nitrogen deficiency in the plant was the limiting factor for normal growth of bolls.

Any explanation for the apparent drop in the rate of absorption of nitrogen as a result of an increased boll load must be made on a purely hypothetical basis. However, one may assume that growth of roots was curtailed in much the same way as growth of shoots was curtailed as boll load increased. The preferential use of available nutrients by developing bolls may account for this relationship. Thus, respiratory energy which is associated with meristematic cells was probably decreased. Since energy is probably required for the absorption of most ions (36), the rate of absorption of the nitrate ion in this experiment could have been considerably reduced.

If the nutritional relations found in this experiment are indicative of those that normally occur, the rate of nitrogen absorption may be the limiting factor for increased retention of normal sized bolls.

Effects of Moisture, Nitrogen, and Gibberellic Acid Treatments on Seed and Fiber Properties

As stated previously, the plants were inadvertently defoliated on October 24 in 1959, while no defoliant was applied in 1960. The first killing frost occurred on November 16 in 1960. If a defoliant is applied when bolls are approximately 35 days of age, seed and lint properties are not appreciably affected (6). Thus, even though there was a difference of 22 days between the date of application of the defoliant in 1959 and the killing frost in 1960, the majority of the bolls picked at the last picking date were probably formed before September 20 during both years.

Immature bolls were probably harvested at the last picking date. Changes in seed and fiber properties that resulted from these immature bolls will be one of the areas for study in this section. The GA treatments in 1960 usually resulted in adverse seed and fiber properties compared to the control. Therefore, comparisons of seed and fiber properties between different periods during the growing seasons (mean for periods) will be primarily limited to the 1959 data.

Seed Properties

The number of seeds per boll was reduced by the I-D treatment during both 1959 and 1960 (Tables 19 and 20, respectively). The N-0 treatment also caused a reduction in the number of seeds per boll during

Table 19. Average number of seeds per boll for various periods during the growing season as affected by moisture and nitrogen, 1959.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
Moisture				
Dry (I-D)	25.5	27.8	31.5	28.3
Medium (I-M)	27.5	32.7	34.7	31.6
Wet (I-W)	28.7	31.8	33.5	31.4
Nitrogen				
No N (N-0)	27.5	29.8	33.2	30.2
100 lb. N/acre (N-100)	27.2	31.2	33.3	30.5
200 lb. N/acre (N-200)	27.1	31.3	33.2	30.6
L.S.D. --5% level (N treatments)	N.S.	N.S.	N.S.	N.S.
Mean for periods	27.3	30.8	33.2	
	L.S.D. (5% level) = 1.1			

Table 20. Average number of seeds per boll for various periods during the growing season as affected by moisture, nitrogen, and gibberellic acid (whole plant treatments), 1960.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
Moisture				
Dry (I-D)	26.6	25.7	31.0	27.8
Medium (I-M)	27.5	29.1	32.1	29.6
Wet (I-W)	29.4	28.5	30.8	29.6
Nitrogen				
No N (N-0)	27.2	26.8	31.3	28.4
100 lb. N/acre (N-100)	27.8	28.1	31.0	29.0
200 lb. N/acre (N-200)	28.5	28.4	31.5	29.5
L.S.D.--5% level (N treatments)	0.8	0.9	N.S.	0.5
Gibberellic acid				
Control (GA-0)	28.4	28.5	32.2	29.7
Potassium salt (GA-1)	26.9	27.3	30.5	28.2
Butyl-cellosolve ester (GA-2)	28.2	27.5	31.2	29.0
L.S.D.--5% level (GA treatments)	0.9	N.S.	0.8	0.5
Mean for periods	27.9	27.8	31.3	
	L.S.D. (5% level) = 0.6			

1960 (Table 20), but no significant difference was found between nitrogen treatments during 1959 (Table 19). The I-D treatment was apparently much more effective than the N-0 treatment in reducing the number of seeds per boll.

The effects of moisture and nitrogen on seed index (weight of 100 seeds), which is a measure of seed size, are presented in Tables 21 and 22 for 1959 and 1960, respectively. Plants grown at the I-D treatment during 1960 were able to maintain a seed index comparable to other moisture treatments, probably because more seeds were aborted per boll (compare Tables 20 and 22). The more severe I-D treatment during 1959 compared to 1960 did not allow the seed index to approach that of the other moisture levels (Table 21). Nitrogen treatments did not appreciably affect the seed index, although there was a significant reduction for the over-all season due to the N-0 treatment during 1959.

Gibberellic acid treatments reduced both the number of seeds per boll (Table 20) and seed index (Table 22). This relationship was probably due to the increased boll load induced by these treatments. The GA-1 treatment was more severe in its action than GA-2.

When the growing season as a whole is considered, the number of seeds per boll increased as the season progressed (Table 19), but the seed index was not affected (Table 21). This relationship suggests

Table 21. Average seed index (weight of 100 seeds) for various periods during the growing season as affected by moisture and nitrogen, 1959.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	grams	grams	grams	grams
Moisture				
Dry (I-D)	12.6	12.8	13.1	12.9
Medium (I-M)	13.9	13.4	13.2	13.5
Wet (I-W)	13.9	13.6	13.4	13.7
Nitrogen				
No N (N-0)	13.2	13.3	13.1	13.2
100 lb. N/acre (N-100)	13.5	13.2	13.2	13.3
200 lb. N/acre (N-200)	13.7	13.3	13.5	13.5
L.S.D.--5% level (N treatments)	0.4	N.S.	N.S.	0.2
Mean for periods	13.5	13.3	13.2	
	L.S.D. (5% level) = N.S.			

Table 22. Average seed index (weight of 100 seeds) for various periods during the growing season as affected by moisture, nitrogen, and gibberellic acid (whole plant treatments), 1960.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	grams	grams	grams	grams
Moisture				
Dry (I-D)	12.5	13.5	14.0	13.3
Medium (I-M)	13.0	12.7	13.9	13.2
Wet (I-W)	12.6	12.4	13.5	12.9
Nitrogen				
No N (N-0)	12.6	13.0	13.6	13.1
100 lb. N/acre (N-100)	12.8	12.7	14.0	13.1
200 lb. N/acre (N-200)	12.8	12.9	13.9	13.2
L. S. D. --5% level (N treatments)	N. S.	0.2	0.2	N. S.
Gibberellic acid				
Control (GA-0)	13.1	13.4	13.8	13.4
Potassium salt (GA-1)	12.3	12.5	13.9	12.9
Butyl-cellosolve ester (GA-2)	12.7	12.7	13.8	13.1
L. S. D. --5% level (GA treatments)	0.3	0.3	N. S.	0.2
Mean for periods	12.7	12.9	13.8	
	L. S. D. (5% level) = 0.2			

that an inadequate supply of nutrients may have caused an increased number of aborted ovules early in the season, compared to later in the season. However, the remaining ovules that developed early in the season evidently received sufficient nutrients to mature into seed which were comparable in size to seed produced later in the season.

Boll Size

Boll size (number of bolls per pound) is dependent on the total weight of seeds and lint per boll. Wadleigh (49) found that both boll size and weight of lint per boll are positively correlated with the weight of seeds per bolls. Thus, the weight of seeds per boll is primarily responsible for variations in boll size.

The effect of treatments on boll size during 1959 and 1960 are presented in Tables 23 and 24, respectively. Most of these effects were discussed earlier in conjunction with yield since boll size is one of the important components of yield. Boll size was definitely decreased by the I-D treatment at all periods during both 1959 and 1960. Nitrogen treatments did not affect boll size in 1959, but during 1960 there was a tendency for boll size to increase as nitrogen levels increased. This relationship reached significance when the entire season was considered (Table 24). The increased boll load induced by GA treatments was undoubtedly responsible for the observed reduction in boll size (Table 24). This effect was more pronounced for the GA-2 treatment.

Table 23. Average boll size, calculated as bolls per pound, for various periods during the growing season as affected by moisture and nitrogen, 1959.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	number	number	number	number
Moisture				
Dry (I-D)	90.9	79.0	72.6	80.8
Medium (I-M)	78.1	65.2	64.2	69.1
Wet (I-W)	73.8	66.5	66.7	69.0
Nitrogen				
No N (N-0)	81.2	72.0	67.8	73.7
100 lb. N/acre (N-100)	81.4	69.7	68.7	73.3
200 lb. N/acre (N-200)	80.3	69.0	66.9	72.1
L.S.D.--5% level (N treatments)	N.S.	N.S.	N.S.	N.S.
Mean for periods	80.8	70.2	67.8	
	L.S.D. (5% level) = 3.0			

Table 24. Average boll size, calculated as bolls per pound, for various periods during the growing season as affected by moisture, nitrogen, and gibberellic acid (whole plant treatments), 1960.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	number	number	number	number
Moisture				
Dry (I-D)	85.9	83.8	68.0	79.2
Medium (I-M)	80.4	76.6	66.6	74.6
Wet (I-W)	77.2	81.2	71.5	76.6
Nitrogen				
No N (N-0)	83.7	82.6	68.9	78.4
100 lb. N/acre (N-100)	80.9	80.2	69.0	76.7
200 lb. N/acre (N-200)	78.9	78.8	68.1	75.3
L. S. D. --5% level (N treatments)	2.3	2.5	N.S.	1.2
Gibberellic acid				
Control (GA-0)	77.8	75.6	67.0	73.5
Potassium salt (GA-1)	85.4	83.7	69.9	79.7
Butyl-cellosolve ester (GA-2)	80.4	82.3	69.1	77.3
L. S. D. --5% level (GA treatments)	3.2	3.5	1.7	1.7
Mean for periods	81.2	80.6	68.7	
	L. S. D. (5% level) = 2.1			

The smaller bolls formed in late June and July (Table 23) were probably due to intense competition for available nutrients due to such factors as vegetative growth and development of the existing boll load.

Lint Index and Lint Percentage

The I-D treatment reduced the seasonal mean for lint index (weight of lint per 100 seeds) in 1959 (Table 25) and increased this mean in 1960 (Table 26). There was also a tendency for GA treatments to reduce the lint index, especially during August (Table 26). Nitrogen treatments had very little effect on this property. One may recall that seed index also varied in much the same way as a result of treatment effects (Tables 21 and 22). Such trends again indicate the close relationship between seed size and lint produced.

The effects of treatments on lint percentage are shown in Tables 27 and 28 for 1959 and 1960, respectively. Lint percentage is an expression of the ratio between the weight of lint and seed cotton in a sample. Although there is a close relationship between seed size and lint produced, a change in one does not necessarily cause a proportionate change in the other. This is shown by the fact that lint percentage followed almost exactly inverse trends that were evident for seed index (seed size)(Tables 21 and 22).

Lint index and lint percentage increased as the season progressed until September at which time both factors decreased (Tables 25 and 27).

Table 25. Average lint index (weight of lint per 100 seeds) for various periods during the growing season as affected by moisture and nitrogen, 1959.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	grams	grams	grams	grams
Moisture				
Dry (I-D)	6.8	8.1	7.1	7.3
Medium (I-M)	7.4	8.0	7.2	7.6
Wet (I-W)	7.6	7.9	7.0	7.5
Nitrogen				
No N (N-0)	7.2	8.0	7.2	7.5
100 lb. N/acre (N-100)	7.2	8.1	7.0	7.4
200 lb. N/acre (N-200)	7.3	8.0	7.2	7.5
L. S. D. --5% level (N treatments)	N. S.	N. S.	N. S.	N. S.
Mean for periods	7.3	8.0	7.1	
	L. S. D. (5% level) = 0.2			

Table 26. Average lint index (weight of lint per 100 seeds) for various periods during the growing season as affected by moisture, nitrogen, and gibberellic acid (whole plant treatments), 1960.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	grams	grams	grams	grams
Moisture				
Dry (I-D)	7.5	7.9	7.7	7.7
Medium (I-M)	7.7	7.7	7.3	7.6
Wet (I-W)	7.5	7.4	7.3	7.4
Nitrogen				
No N (N-0)	7.5	7.7	7.6	7.6
100 lb. N/acre (N-100)	7.6	7.6	7.4	7.5
200 lb. N/acre (N-200)	7.5	7.7	7.3	7.5
L. S. D. --5% level (N treatments)	N. S.	N. S.	0.1	N. S.
Gibberellic acid				
Control (GA-0)	7.6	7.9	7.4	7.6
Potassium salt (GA-1)	7.6	7.6	7.5	7.5
Butyl-cellosolve ester (GA-2)	7.5	7.5	7.3	7.4
L. S. D. --5% level (GA treatments)	N. S.	0.2	N. S.	0.1
Mean for periods	7.6	7.7	7.4	
	L. S. D. (5% level) = 0.1			

Table 27. Average lint percentage for various periods during the growing season as affected by moisture and nitrogen, 1959.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
Moisture				
Dry (I-D)	35.2	38.8	35.1	36.4
Medium (I-M)	34.8	37.5	35.5	35.9
Wet (I-W)	35.3	36.7	34.2	35.4
Nitrogen				
No N (N-0)	35.4	37.7	35.4	36.1
100 lb. N/acre (N-100)	35.0	37.9	34.6	35.8
200 lb. N/acre (N-200)	34.9	37.5	34.8	35.7
L.S.D. --5% level (N treatments)	N.S.	N.S.	N.S.	N.S.
Mean for periods	35.1	37.7	34.9	
L.S.D. (5% level) = 0.5				

Table 28. Average lint percentage for various periods during the growing season as affected by moisture, nitrogen, and gibberellic acid (whole plant treatments), 1960.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
Moisture				
Dry (I-D)	37.6	37.0	35.4	36.7
Medium (I-M)	37.0	37.8	34.5	36.4
Wet (I-W)	37.4	37.3	34.9	36.5
Nitrogen				
No N (N-0)	37.5	37.2	35.7	36.8
100 lb. N/acre (N-100)	37.3	37.5	34.6	36.5
200 lb. N/acre (N-200)	37.2	37.4	34.5	36.4
L. S. D. --5% level (N treatments)	N. S.	N. S.	0.3	0.2
Gibberellic acid				
Control (GA-0)	36.5	37.1	35.0	36.2
Potassium salt (GA-1)	38.3	37.7	35.1	37.0
Butyl-cellosolve ester (GA-2)	37.2	37.3	34.8	36.4
L. S. D. --5% level (GA treatments)	0.6	0.4	N. S.	0.3
Mean for periods	37.3	37.4	35.0	
	L. S. D. (5% level) = 0.3			

Such a drop in September was probably due to bolls that did not mature fully as a result of the shortened growing period caused by the defoliation in 1959.

Fiber Length

The effects of moisture and nitrogen treatments on the upper half mean length (UHM) of fibers are presented in Tables 29 and 30 for 1959 and 1960, respectively. Since turgor is necessary for the expansion and elongation of any cell, one would expect a reduction in fiber length due to moisture stress as others have found (16, 47). Such a trend was evident for the I-D treatment at the different periods during 1959; however, the less severe I-D treatment in 1960 did not reduce fiber length. Nitrogen treatments did not affect the UHM to any appreciable degree during either year, especially when the entire season was considered. The lack of a nitrogen response on fiber length was also observed by Hamilton et al. (23).

The increased boll load that was induced by GA treatments resulted in significant decreases in UHM, especially during August (Table 30). Such a relationship emphasizes the importance of the protoplasm of young lint cells in the elongation process since functions of the protoplasm were undoubtedly curtailed as a result of the drain on available nutrients.

Table 29. Average upper half mean length (UHM) of fibers for various periods during the growing season as affected by moisture and nitrogen, 1959.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	inches	inches	inches	inches
Moisture				
Dry (I-D)	1.002	1.023	1.013	1.013
Medium (I-M)	1.060	1.041	1.020	1.040
Wet (I-W)	1.048	1.047	1.014	1.036
Nitrogen				
No N (N-0)	1.027	1.055	1.023	1.035
100 lb. N/acre (N-100)	1.033	1.024	1.018	1.025
200 lb. N/acre (N-200)	1.050	1.032	1.008	1.030
L.S.D.--5% level (N treatments)	.018	.016	N.S.	N.S.
Mean for periods	1.037	1.037	1.016	
	L.S.D. (5% level) = N.S.			

Table 30. Average upper half mean length (UHM) of fibers for various periods during the growing season as affected by moisture, nitrogen, and gibberellic acid (whole plant treatments), 1960.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	inches	inches	inches	inches
Moisture				
Dry (I-D)	1.007	1.055	1.064	1.042
Medium (I-M)	1.032	0.996	1.065	1.031
Wet (I-D)	1.025	0.988	1.042	1.018
Nitrogen				
No N (N-0)	1.015	1.031	1.044	1.030
100 lb. N/acre(N-100)	1.025	1.002	1.063	1.030
200 lb. N/acre (N-200)	1.024	1.006	1.065	1.032
L.S.D.--5% level (N treatments)	N.S.	0.011	0.012	N.S.
Gibberellic acid				
Control (GA-0)	1.032	1.029	1.051	1.037
Potassium salt (GA-1)	1.008	1.004	1.064	1.025
Butyl cellosolve ester (GA-2)	1.024	1.006	1.057	1.029
L.S.D.--5% level (GA treatments)	0.014	0.015	N.S.	0.008
Mean for periods	1.021	1.013	1.057	
	L.S.D. (5% level) = 0.010			

As mentioned earlier, many of the bolls which developed in September were probably immature at the time of picking. However, fiber length was not significantly affected during this period in 1959 (Table 29). Such a relationship may be explained by the fact that fiber elongation occurs during approximately the first 21 days of growth of the boll, and most immature bolls that were picked had probably reached this age.

Fiber Strength

There was a general tendency for fiber strength to be greater when developed under the low moisture treatment (I-D) during 1959 and 1960 (Tables 31 and 32, respectively). Such findings agree with the work of Eaton and Ergle (16) who postulated that such a relationship was actually due to an increase in carbohydrates that was associated with drouth. Since a nitrogen deficiency is also associated with increased carbohydrates (49), an increase in fiber strength would have been expected at the N-0 level in this experiment. Although there was a general tendency for increased fiber strength at the N-0 level during both 1959 and 1960, a significant difference was found only in August of 1960 (Table 32). GA treatments (in July and August) were again associated with an adverse effect since fiber strength was significantly reduced by such treatments during August (Table 32).

Table 31. Average strength of fibers for various periods during the growing season as affected by moisture and nitrogen, 1959.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	index	index	index	index
Moisture				
Dry (I-D)	3.58	3.52	3.28	3.46
Medium (I-M)	3.55	3.45	3.25	3.42
Wet (I-W)	3.41	3.45	3.31	3.39
Nitrogen				
No N (N-0)	3.54	3.50	3.32	3.45
100 lb. N/acre (N-100)	3.51	3.45	3.27	3.41
200 lb. N/acre (N-200)	3.49	3.46	3.26	3.40
L.S.D. --5% level (N treatments)	N.S.	N.S.	N.S.	N.S.
Mean for periods	3.51	3.47	3.28	
	L.S.D (5% level) = 0.06			

Table 32. Average strength of fibers for various periods during the growing season as affected by moisture, nitrogen, and gibberellic acid (whole plant treatments), 1960.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	index	index	index	index
Moisture				
Dry (I-D)	3.51	3.58	3.35	3.48
Medium (I-M)	3.43	3.40	3.38	3.40
Wet (I-W)	3.44	3.40	3.30	3.38
Nitrogen				
No N (N-0)	3.46	3.54	3.29	3.43
100 lb. N/acre (N-100)	3.46	3.40	3.37	3.41
200 lb. N/acre (N-200)	3.46	3.43	3.37	3.42
L.S.D. --5% level (N treatments)	N.S.	0.06	0.06	N.S.
Gibberellic acid				
Control (GA-0)	3.49	3.54	3.32	3.45
Potassium salt (GA-1)	3.43	3.43	3.35	3.40
Butyl-cellosolve ester (GA-2)	3.46	3.41	3.36	3.41
L.S.D. --5% level (GA treatments)	N.S.	0.08	N.S.	0.04
Mean for periods	3.46	3.46	3.34	
	L.S.D. (5% level) = 0.05			

Development of the secondary wall is necessary for good fiber strength. Since the secondary wall begins development approximately 21 days after anthesis (25), immature fibers will probably be weak fibers. The weak fibers formed during September (Tables 31 and 32) probably were the result of immature fibers formed during the shortened growing period.

Fiber Fineness

Fibers were finer when grown under the low moisture treatment (I-D) during both 1959 and 1960 (Tables 33 and 34, respectively). This effect was more pronounced in 1959 with the more severe I-D treatment. The preceding section showed that the I-D treatment was associated with increased strength of fibers and thus good secondary wall development. Consequently, the finer fibers produced at this treatment level were probably the result of a smaller perimeter of individual fibers.

Nitrogen treatments did not affect fiber fineness in 1959 (Table 33). In 1960, however, finer fibers were generally produced by the N-0 treatment, although this effect was not consistent throughout the season (Table 34). In general, GA treatments did not materially affect fiber fineness (Table 34). However, the GA-2 treatment produced coarser fibers than the GA-0 treatment during September. Decreases in fiber fineness that occurred during September for all treatments (Tables 33

Table 33. Average fineness of fibers for various periods during the growing season as affected by moisture and nitrogen, 1959.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	index	index	index	index
Moisture				
Dry (I-D)	4.16	4.17	3.52	3.95
Medium (I-M)	4.45	4.36	3.73	4.18
Wet (I-W)	4.45	4.41	3.54	4.13
Nitrogen				
No N (N-0)	4.36	4.28	3.57	4.07
100 lb. N/acre (N-100)	4.31	4.32	3.55	4.06
200 lb. N/acre (N-200)	4.39	4.34	3.67	4.13
L. S. D. --5% level (N treatments)	N. S.	N. S.	N. S.	N. S.
Mean for periods	4.35	4.32	3.60	
	L. S. D. (5% level) = 0.05			

Table 34. Average fineness of fibers for various periods during the growing season as affected by moisture, nitrogen, and gibberellic acid (whole plant treatments), 1960.

Treatment	Approximate period during which bolls developed			
	Late June & July	August	September	Seasonal mean
	index	index	index	index
Moisture				
Dry (I-D)	4.22	4.39	3.85	4.15
Medium (I-M)	4.40	4.48	4.03	4.30
Wet (I-W)	4.39	4.25	3.89	4.18
Nitrogen				
No N (N-0)	4.21	4.47	3.83	4.17
100 lb. N/acre (N-100)	4.38	4.30	3.95	4.21
200 lb. N/acre (N-200)	4.42	4.35	4.00	4.26
L. S. D. --5% level (N treatments)	0.08	0.09	0.09	0.05
Gibberellic acid				
Control (GA-0)	4.35	4.36	3.85	4.19
Potassium salt (GA-1)	4.34	4.40	3.99	4.24
Butyl-cellosolve ester (GA-2)	4.32	4.37	3.93	4.21
L. S. D. --5% level (GA treatments)	N. S.	N. S.	0.09	0.04
Mean for periods	4.34	4.37	3.92	
	L. S. D. (5% level) = 0.07			

and 34) were undoubtedly due to immature fibers produced during that period.

Relationships Between Pollination, Embryo Development and Boll Abscission

Role of Nonviable Pollen

There is no doubt that anything which prevents pollination of cotton flowers will result in the abscission of young bolls from these flowers. Thus, Lloyd (34) found that rain that occurred on the day of anthesis caused the destruction of pollen and young bolls were then abscissed. The importance of nonviable pollen as a cause of boll abscission under ordinary circumstances has not been established. The need for more information on this subject prompted a detailed study.

A histological study of many ovules throughout the growing season showed that most ovules of both normal and abscissed bolls contained embryos. Thus, the author concludes that nonviable pollen is not a primary factor in boll abscission. A typical example of the embryo development of a boll that abscissed at 120 hours after anthesis and a normal boll of the same age is presented in Figure 9-A and Figure 9-B, respectively.

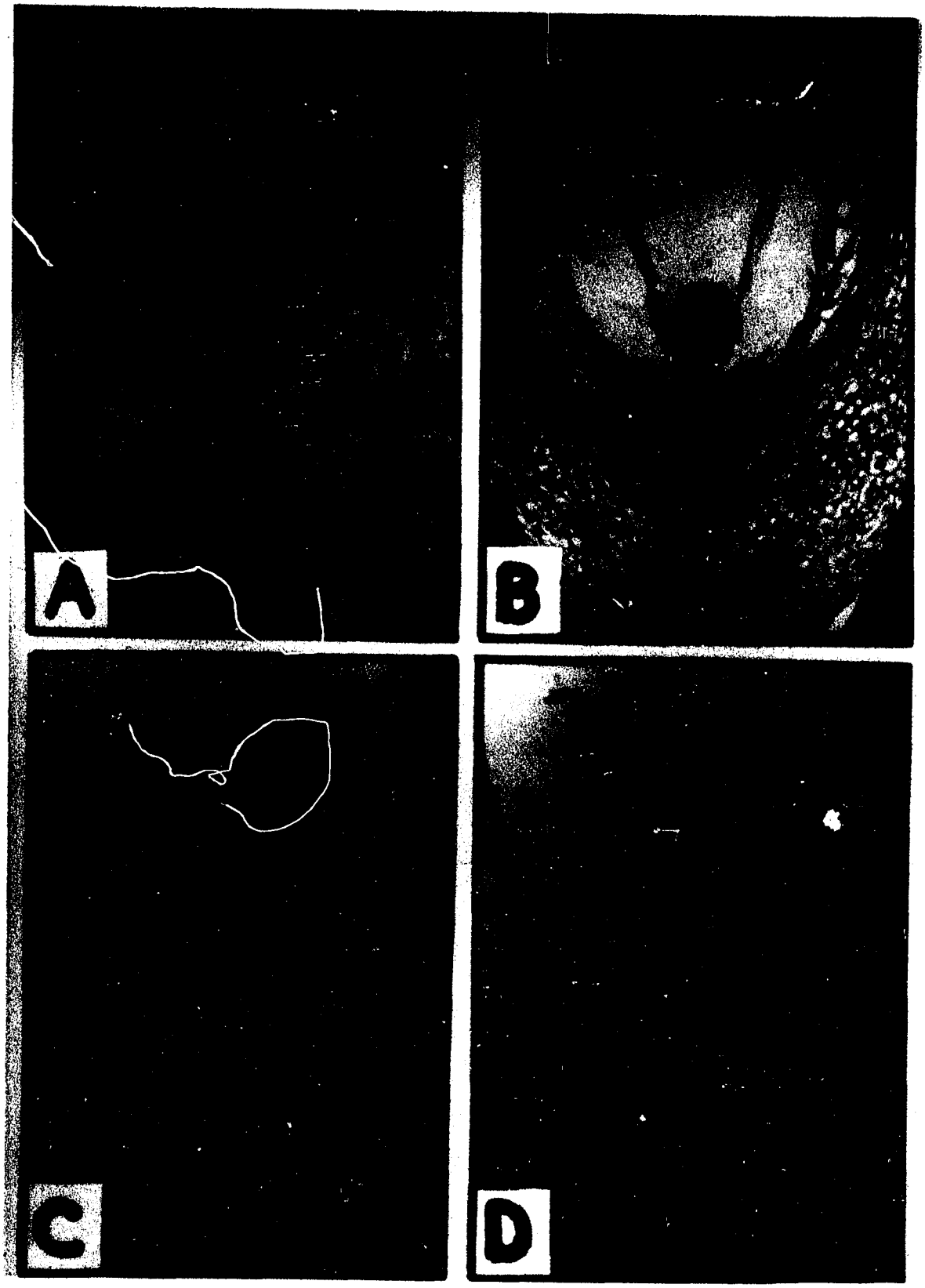
Figure 9. Photomicrographs of cotton ovules (longitudinal sections) showing embryo and endosperm development during periods preceding and including the time of active boll abscission (120 hours after anthesis). All figures approximately 200X.

A - Zygote and free nuclear endosperm, 48 hours after anthesis.

B - Proembryo shortly after active cell division had been initiated, 72 hours after anthesis (note pollen tube in micropylar region).

C - Many-celled proembryo and cellular endosperm from a normal boll, 120 hours after anthesis.

D - Many-celled proembryo of an ovule from a boll that abscissed, 120 hours after anthesis.


A
B
C
D

Embryo Development

Abscission of young bolls was found to occur during a period ranging from 72 to 168 hours after anthesis, but the abscission occurred most frequently between 96 and 120 hours after anthesis. Some of the various stages in the development of the embryo and endosperm during periods preceding and including the time of active boll abscission are shown in Figure 9. At 48 hours after anthesis the free nuclear endosperm had developed quite extensively, but the zygote had not divided (Figure 9-A). At 72 hours after anthesis the proembryo had taken definite form (Figure 9-B). At 120 hours after anthesis the proembryo consisted of many cells and the endosperm had changed to a cellular form (Figure 9-C). A comparison of this embryo with an embryo of the same age from a boll that abscissed (Figure 9-D) shows that growth in terms of cell division was very similar. This relationship seemed to be typical, indicating that embryo development proceeds normally up to the time of abscission.

Controlled Pollination Studies

When pollination was prevented by mechanical means, most of the unfertilized young bolls abscissed between 96 and 120 hours after anthesis. This period of time was remarkably similar to that required for boll abscission when pollination was not a factor. Such a relationship is further evident from a study of fresh weights of fertilized and

unfertilized bolls at different periods after anthesis (Table 35). Growth of unfertilized bolls was equivalent to that for normal fertilized bolls at 48 hours after anthesis. However, beginning at 72 hours after anthesis, the rate of growth of unfertilized bolls increased very little as compared to normal fertilized bolls. These results are similar to those found by Mason (39). The weight of fertilized bolls that abscissed at 96 and 120 hours after anthesis was very similar to that found for unfertilized bolls at these periods.

The relationships described indicate that a common mechanism may be responsible for the abscission of both fertilized and unfertilized bolls. Such a mechanism evidently becomes active simultaneously with a reduction in growth of bolls. In this experiment a reduction in the rate of growth of unfertilized bolls was first observed 72 hours after anthesis, and one may assume that fertilized bolls that abscissed followed a similar pattern of growth.

Relationships Between Abscission and Auxin Concentration of Bolls

As stated previously, young bolls are particularly immune to abscission from a period ranging from the day of anthesis to approximately 48 hours after anthesis. Older buds also appear to be immune to abscission up to the time of anthesis. Also, the preceding study

Table 35. A comparison of fresh weights of normal fertilized bolls, unfertilized bolls that abscissed[1] and fertilized bolls that abscissed[1]. Bolls collected during August, 1960.

Type of boll	Age of bolls in hours after anthesis			
	48	72	96	120
	Average weight in grams per boll			
Normal fertilized	1.3	1.8	2.2	2.9
Unfertilized that abscissed	1.4	1.6	1.6	2.0
Fertilized that abscissed	---	---	1.6	1.8

[1] Abscission occurred at 96 and 120 hours after anthesis.

showed that fertilization became critical for continued growth of bolls approximately 72 hours after anthesis. This period of time corresponded closely to the time when embryo development was initiated. However, growth of fertilized bolls that eventually abscissed was not stimulated by fertilization. These relationships suggest that a growth hormone, such as an auxin, was controlling these processes. This experiment was designed to study these relationships more thoroughly.

A comparison of the auxin concentration of normal bolls of different ages in hours after anthesis showed that auxin concentration was high at 48 hours, but dropped at 72 hours, and started to increase again at 96 hours (Table 36). Such a drop in auxin concentration for normal bolls at 72 hours after anthesis may be due to an inhibitor such as the one described by Carns et al. (8). The auxin concentration for fertilized bolls that abscissed at 96 hours after anthesis was variable but appeared to be lower than that found for normal fertilized bolls at 72 hours after anthesis (Table 36).

With the above facts in mind, a hypothetical account of the role of auxin in the boll abscission process may be advanced. Auxin concentration of young bolls is high during a period from anthesis to 48 hours after anthesis. Pollination may account for this relationship (42). At 72 hours after anthesis the auxin concentration drops to a level below which abscission would occur due, perhaps, to an increase in inhibitor concen-

Table 36. A comparison of the amount of extractable auxin obtained from normal and abscissed cotton bolls as determined by the Avena test. Standard errors are given in parentheses.

Experiment	IAA Standard (50 µg/liter)	Normal bolls			Fertilized bolls that abscissed
		Age (hours after anthesis)			Age (hours after anthesis)
		48	72	96	96
		Curvature in degrees			
1	12.2(0.72)	17.7(1.29)	12.8(1.06)	15.6(0.85)	5.82(1.72)
2	17.1(1.36)	17.4(0.80)	13.9(1.32)	15.9(1.22)	10.89(0.71)

Table 36. A comparison of the amount of extractable auxin obtained from normal and abscissed cotton bolls as determined by the Avena test. Standard errors are given in parentheses.

Experiment	IAA Standard (50 µg/liter)	Normal bolls			Fertilized bolls that abscissed
		Age (hours after anthesis)			Age (hours after anthesis)
		48	72	96	96
		Curvature in degrees			
1	12.2(0.72)	17.7(1.29)	12.8(1.06)	15.6(0.85)	5.82(1.72)
2	17.1(1.36)	17.4(0.80)	13.9(1.32)	15.9(1.22)	10.89(0.71)

tration. Thus, any additional drop in auxin concentration promotes abscission and provides a means for the plant to eliminate bolls that would be malformed due to inadequate nutrition. An additional drop in auxin concentration may occur as a result of an inadequate supply of nutrients to young bolls. A low nitrogen supply, for instance, could in turn limit the supply of precursors (such as tryptophan) needed for auxin production. Thus, those bolls that are in a favorable position to receive adequate nutrition are able to withstand the period of low auxin concentration and are essentially immune to abscission from this period until maturation.

SUMMARY

Moisture, nitrogen, and gibberellic acid variables were used to form basic experiments for a detailed study of boll abscission in cotton. The effects of these treatments on fiber properties and other plant characteristics were also studied. Experiments were conducted to study the relationships between pollination and boll abscission and the role of auxin in the abscission process.

A summary of the findings of these studies is as follows:

1. Nitrate-nitrogen concentrations of petioles (taken to be indicative of the nitrogen status of the cotton plant) decreased as the growing season advanced at all moisture levels regardless of the amount of nitrogen applied. However, plants that received nitrogen fertilizer maintained higher nitrate levels throughout the season than plants grown under a nitrogen deficiency.

2. The effects of different moisture levels on boll set were not clear. There was some indication that boll set was immediately increased by an irrigation at the lowest moisture level. However, since the uptake of nitrogen was also increased by an irrigation at this level, moisture effects may have been secondary.

3. When vegetative growth was increased by nitrogen fertilization, percentage boll abscission also increased, indicating that vegetative growth was dominant to boll set.

4. Nitrogen fertilization was associated with a high nitrate-nitrogen concentration in the plant early in the season. This favored vegetative growth but not boll set. As the boll load became greater, the nitrate-nitrogen concentration of the plant decreased and the number of bolls that set at weekly intervals increased.

5. When gibberellic acid (GA) was sprayed on whole plants at the rate of 18 grams of GA in 48 gallons of water per acre, percentage boll abscission was decreased and the number of bolls that set per plant was increased. However, increased boll set was apparently offset by decreased boll size, and yields were not increased.

6. Treatment of individual flowers with 100 ppm GA at daily intervals resulted in smaller plants with a much heavier boll load than the control. Boll size was extremely reduced by such treatments. Chemical analyses of leaves and petioles showed that nitrogen was evidently limiting for normal growth of bolls.

7. Plants grown under the nitrogen deficiency imposed were apparently able to adjust growth and fruiting so that seed and fiber properties were not greatly affected.

8. A low moisture level had an adverse effect on the number of seeds per boll, boll size, and fiber fineness. There was a tendency for fiber strength to be increased by this treatment. Other boll or fiber characters were not affected.

9. The increased boll load and increased growth that resulted from GA treatments also reduced the size of seed and the quality of fiber produced.

10. When the entire season was considered, bolls that formed in late June and July had fewer seed per boll and bolls were smaller than bolls produced later in the season. The shortened growing period at the end of the season caused a reduction in lint index, strength, and fineness for bolls that were formed in September.

11. Histological studies showed that most ovules of both normal and abscissed bolls contained embryos, indicating that boll abscission was not ordinarily caused by nonviable pollen. Embryo development was initiated approximately 72 hours after anthesis and was apparently normal up to the time of abscission.

12. The process of fertilization appeared to be necessary for boll growth following a 72-hour period after anthesis. Growth of bolls that abscissed was not stimulated by fertilization.

13. Auxin concentrations of normal bolls of different ages in hours after anthesis were highest at 48 hours, dropped sharply at 72

hours and started to increase again at 96 hours. The auxin concentration for fertilized bolls that abscissed at 96 hours after anthesis was lower than the auxin concentration for normal bolls at 72 hours after anthesis.

CONCLUSIONS

From the evidence presented it is concluded that the boll abscission process acts as a protective device to prevent overfruiting and the production of small inferior bolls. This is in opposition to the widely-held assumption that the abscission of bolls is normally excessive.

Boll abscission must be an outward expression of a much more complex sequence of events that involves the nutrition of the plant. Evidence presented here and by other workers points to nitrogen as the nutrient that becomes limiting in the plant for increased boll set. A more thorough study of this aspect of boll abscission seems to be warranted.

Growth regulators such as gibberellic acid offer hope for greater scientific control of fruiting and growth of cotton plants. Their use seems to be contingent upon more efficient plants with a greater fruiting capacity. At present, gibberellic acid is a valuable research tool that can be effectively used by plant breeders and physiologists.

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