Published November, 1967

# Boll Retention in Relation to Leaf and Boll Development in Cotton (*Gossypium hirsutum* L.)[1]

R. E. Johnson and F. T. Addicott[2]


## ABSTRACT

The effect of leaf area and gibberellic acid (GA) on boll retention was studied on cotton plants growing in nutrient culture. Leaf area was reduced to approximately half the control by two methods of leaf clipping, and two concentrations of GA were applied to all flowers.

In control plants, the ratio of leaves to retained bolls was initially high. It declined to approximately three at midseason, and thereafter remained constant to the end of the fruiting period. After adjustments for differences in leaf size, ratios for partially defoliated plants were similar to those of the control. Percent boll retention paralleled leaf-boll ratios.

Seed cotton yield and percent retention were significantly reduced in the partially defoliated treatments; however, no differences were found when seed cotton yield was expressed as a function of maximum leaf area developed. There were no differences between the GA treatments and control for any of the characters measured. That retention was not increased by treating all the flowers contrasts with results obtained when only a few flowers or young bolls were treated.

The number of seeds per retained boll for all treatments was low initially, increasing to a maximum at the time of greatest shedding. This may indicate that a high seed complement is required for a boll to be retained when competition for assimilate occurs.

The results are interpreted as supporting the view that boll retention depends on the presence of a sufficient number of developing seeds to mobilize the assimilates required for continued growth, and upon the availability of assimilates as governed by the vegetative-reproductive status of the plant.


*Additional index words:* leaf area, boll abscission, gibberellic acid, vegetative-reproductive interactions, fruiting efficiency.

FIELD-GROWN Upland cotton (*Gossypium hirsutum* L.) normally retains only 30 to 40% of the flowers that reach anthesis. Since there is a potential reduction in yield of the crop through the shedding of 60 to 70% of the young fruits, the subject of boll shedding has received the attention of many investigators. Studies have indicated that many factors, including temperature, soil moisture, mineral nutrition, light, genotype, boll load, applied growth regulators, and insect damage, affect the rate and amount of shedding. Eaton (6) and Hall (9) have reviewed the extensive literature.

Early studies (5, 10, 11, 13) indicated that nutritional factors can be closely associated with boll shedding. However, Eaton and Ergle (7) found only small differences in patterns of carbohydrate and nitrogen accumulation among plants which were shedding at different rates, or between control plants and plants which were sprayed with sucrose, urea, or both. On the basis of the results, they discounted nutritional interpretations and suggested that hormonal interactions were primarily responsible for boll shedding.

It has been demonstrated that fertilization and seed development are required for a boll to be retained. Crane (2) has put forth the view that, upon fertilization, a stimulus is created that establishes a high metabolic gradient between ovules and ovaries on one hand and vegetative organs on the other. The gradient diverts the flow of food materials from vegetative organs and produces, in short, a mobilization effect. Dale and Milford (3) have expressed a somewhat similar view, that fertilization in cotton sets in motion a nutritional polarity of a unique kind, and shedding results if this polarity is not established or maintained.

The fact that the highest shedding rates occur under low light conditions [through artificial shading or clouds (5)] or late in the season when plants are supporting a heavy boll load indicates that the availability of assimilates may be an important factor limiting boll retention. Thus, the key factors in retention appear to be the mobilization of assimilates, initiated by hormonal action at fertilization, and the availability of assimilates as governed by the growth status of the entire plant.

The objectives of this study were to observe the effect of leaf area development on boll retention, as well as changes in retention resulting from application of gibberellic acid (GA) to all the flowers.

## MATERIALS AND METHODS

Cotton was grown at Davis, Calif., during the summer of 1965. Seed of a component line (Family 77) of 'Acala 4-42' was furnished by the U.S. Cotton Research Station, Shafter, Calif. Plants were started in the greenhouse in half-gallon milk cartons in early April. Special attention was given during early growth to select plants uniform in size and development. After 6 weeks, the plants were taken to a lath house for 2 weeks, then transplanted to 10-gallon containers (52 cm high $\times$ 32 cm diameter) filled with well-settled vermiculite. The containers were placed outdoors, 1.07 m apart, on a concrete slab and watered every other day with an excess of half-strength Hoagland's solution (chelated iron source) with pH adjusted to 6.7. Tap water was used on alternate days. To increase uniformity, vegetative branch buds at the cotyledonary node were pinched off and fruiting behavior was observed on the vegetative (monopodial) branches above the cotyledonary node and on the fruiting (sympodial) branches. In all treatments, including control, two-thirds (64 to 67%) of the total bolls were borne on the fruiting branches. The first flowers appeared during the third week of June. Insecticides were applied frequently, and insect damage was practically nil.

Flowers were tagged on the day of anthesis throughout the flowering period by placing dated tags on the fruiting branch proximal to the flower pedicel. Weekly measurements of height, number of nodes, and number of leaves over 6 cm in length were made from early June to mid-September, by which time flowering had ceased. Mean leaf size was estimated periodically, using the method of Ashley, Doss, and Bennett (1). This method, based on measurements of length and width and the multiplication of their product by a factor ($A = L \times W \times$ factor), allows the estimation of leaf area without sacrifice of plants.

Five plants (one plant/can) were used for each treatment in a randomized complete block arrangement. The concentrations of GA used were 25 and 100 ppm. Solutions (0.2 ml) were applied with a hypodermic syringe inside at the bottom of each flower on the day of anthesis. The total mean amount of GA applied per plant was 0.434 mg for the 25-ppm treatment and 1.772 mg for the 100-ppm treatment. Leaf area was reduced to

[1] Contribution of the Agronomy Department, University of California, Davis. Received July 25, 1967.

[2] Assistant Specialist and Professor of Agronomy, Davis, Calif.

approximately half that of the control by one of two patterns of leaf clipping. Beginning with the mainstem leaf at the node of the first fruiting branch, alternate leaves acropetally were removed or half of each leaf was removed by cutting along the midrib with a razor blade. Leaf cuts and removals were made twice weekly on leaves attaining a length of 6 cm. Control plants were untreated.

Each plant was mapped after flowering had ceased. For each fruiting position, the flowering date was recorded, as well as the presence of absence of a boll, or whether the flower bud had abscised before reaching anthesis. Bud shedding was low, ranging from 14 to 17% of total fruit forms that would have reached anthesis by early September. Seed cotton was collected individually from open bolls at harvest, and the number of locules per boll was recorded. Individual bolls were ginned on a small roller gin, and weight of boll and seeds and number of seeds were noted.

## RESULTS

Cumulative totals of flowers and bolls from GA treatments and controls give curves that are quite similar (Fig. 1). Also, no significant differences were found between GA-treated and control plants for seed cotton yield, flower and boll numbers, percent retention, height, or maximum leaf area developed (Table 1). Likewise, there were no differences in seeds/boll, seed weight, lint percent, or weight/boll (data not shown). Before August 1, bolls accumulated at almost the same rate as flowers, indicating that very little shedding occurred. After August 1, bolls accumulated at a reduced rate, whereas flower number continued to increase at an undiminished rate until late August.

Cotton normally produces flowers over an 8- to 12-week period. During this period the distribution of growth between vegetative and reproductive portions of the plant is continually changing. An estimate of the distribution was obtained throughout the fruiting period by calculating the leaf-boll ratio, i.e., the number of leaves per retained boll. At the time the first flower opened 10 to 15 leaves were present, accounting for an initially high ratio. As the flowering rate increased, the ratio declined to 2.5 to 3.5 at midseason, and remained relatively constant thereafter (Fig. 2, 3).

**Table 1. Plant means of various growth and yield characters for each treatment.**

| Treatment | Mean per plant: Seed cotton | Total flowers | Total bolls | Seasonal boll retention | Height | Maximum leaf area | Seed cotton /dm² leaf area* |
|---|---|---|---|---|---|---|---|
| | g | | | % | cm | dm² | g |
| Control | 369 | 93 | 47 | 51.1 | 128 | 85.6 | 4.32 |
| 25 ppm GA | 339 | 88 | 45 | 51.2 | 123 | 74.8 | 4.53 |
| 100 ppm GA | 348 | 89 | 47 | 53.6 | 119 | 74.1 | 4.71 |
| Alt. leaves removed | 233 | 75 | 30 | 40.5 | 90 | 50.8 | 4.69 |
| 1/2 each leaf removed | 287 | 88 | 35 | 40.9 | 101 | 56.7 | 5.15 |
| LSD .05 | 63 | NS | 4 | 3.4 | 21 | 12.1 | NS |

* Grams seed cotton/maximum leaf area (Aug. 31).

Curves for percent retention and leaves/boll for control plants are shown in Fig. 2. Percent retention was calculated for the 5-day period just before the leaf-count date. The shape of the retention curve is very similar to the leaf-boll curve. Percent retention at high, intermediate, and low leaf-boll ratios for all treatments is given in Table 2.

Figure 3 gives leaf-boll ratios for control and partially defoliated treatments. Because of differences in leaf size, adjustments were made in leaf number for the partially defoliated treatments before calculating ratios. The adjustments were based on leaf area/plant, with the leaf number adjusted so that mean leaf size was the same as that of the control plants. The ratios in partially defoliated treatments and in the control were initially high. They declined to a relatively constant level during the latter part of the fruiting period. Seed cotton yield per plant and seasonal boll retention were significantly less for both partially defoliated treatments than for the control (Table 1). However, when seed cotton yield was expressed as a function

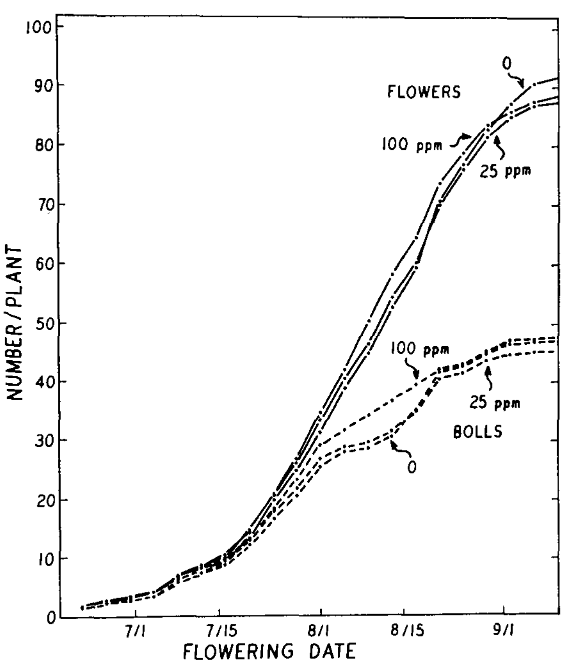


**Fig. 1. Cumulative totals of flowers and bolls for control plants and plants treated with GA applied in the flower on the day of anthesis, throughout the flowering period.**

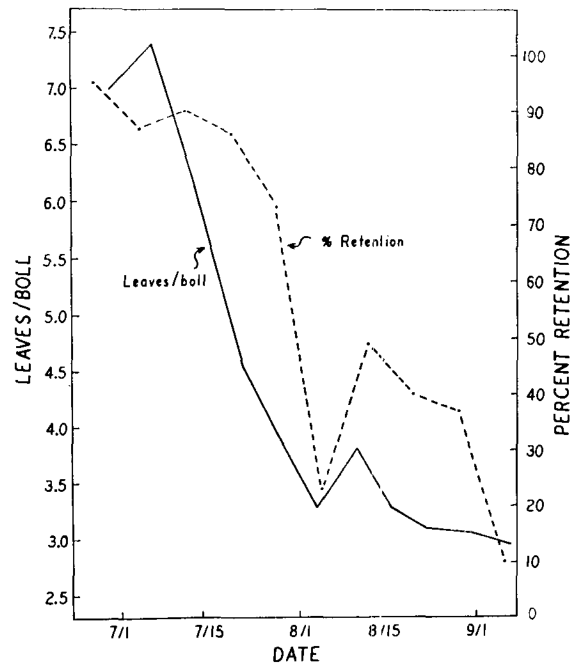


**Fig. 2. Ratio of leaves to set bolls, and boll retention percentages throughout the flowering period for control plants. Retention percentages are based on total bolls retained during a 5-day period.**

**Table 2. Percent retention of bolls at various leaf/boll ratios.**

| Treatment | % retention* | | |
|---|---|---|---|
| | Leaf/boll ratio | | |
| | > 8.0 | 4.0-7.9 | < 3.9 |
| Control | 90.8 | 68.2 | 32.4 |
| Alternate leaves removed† | 88.3 | 71.7 | 31.2 |
| 1/2 each leaf removed† | | 63.8 | 32.6 |
| 25 ppm GA | 91.2 | 70.7 | 34.5 |
| 100 ppm GA | 91.7 | 90.1 | 38.4 |

* % retention of bolls from flowers opening during a 5-day period preceding the date leaves were counted. † Mean leaf size adjusted to control prior to calculating ratio (see text).

of maximum leaf area developed, there were no significant differences. Leaf/boll curves for the GA treatments (not shown) were practically identical to those of the controls.

The influence on retention of the proximity of a leaf to a fruiting position is shown in Table 3. The data, taken from the alternate-leaf-removal treatment, indicate retention at the fruiting positions subtended by a leaf approached that of control plants, whereas retention was reduced at positions not subtended by a leaf.

Mean number of seeds/retained boll are shown for control plants only (Fig. 4), as values did not differ significantly among treatments. Number of seeds per boll was low for the first bolls set; it increased to a maximum in mid-August when shedding was greatest. The increased seed number resulted from more seeds per locule and more locules per boll. Only 10.1% of bolls set after August 1 contained four locules (the rest had five), compared to 55.7% for bolls set before August 1. Mean seeds per locule was 6.70 ± 0.18 for bolls set before August 1 and 8.15 ± 0.07 for bolls set after August 1. The seed complement of bolls shed is not known. However, assuming that the same relative number of four- and five-locule bolls differentiated throughout the season, the data indicate differential retention in favor of five-locule bolls during the latter half of the fruiting period when shedding is greatest.

**Table 3. Percent retention, based on means of five plants, of bolls with or without a subtending leaf at the fruiting position.**

| Flowers opening: | % retention | | |
|---|---|---|---|
| | Subtending leaf present | Subtending leaf removed | Control plants; no leaves removed |
| Before 7/31 | 73.0 | 56.1 | 80.9 |
| After 8/1 | 32.1 | 21.7 | 37.9 |
| All season | 45.0 | 33.1 | 51.1 |

## DISCUSSION

That retention was not increased when GA was applied to all the flowers contrasts with earlier results obtained with single applications. In our experiment the time of application relative to anthesis was different from that reported by others (4, 14), in that the solutions were applied inside at the bottom of the flower on the day of anthesis. Walhood (14) treated 1- to 4-day old bolls and Dransfield (4) treated 3-day old bolls. Their solutions were applied in the cup-like calyx after removal of the corolla. We do not believe that differences in time or placement account for the different results, since other short-term experiments by one of the authors (R.E.J., unpublished) have shown flower treatment to be as effective as boll treatment. The different results obtained probably were due to the fact that all flowers were treated in this experiment, while only isolated bolls were treated in the other studies.

We believe the increased retention from single applications could have been brought about by enhancement of the ability of the treated bolls to attract assimilate, thereby gaining a competitive advantage over nontreated bolls. Seth and Wareing (12) have demon-

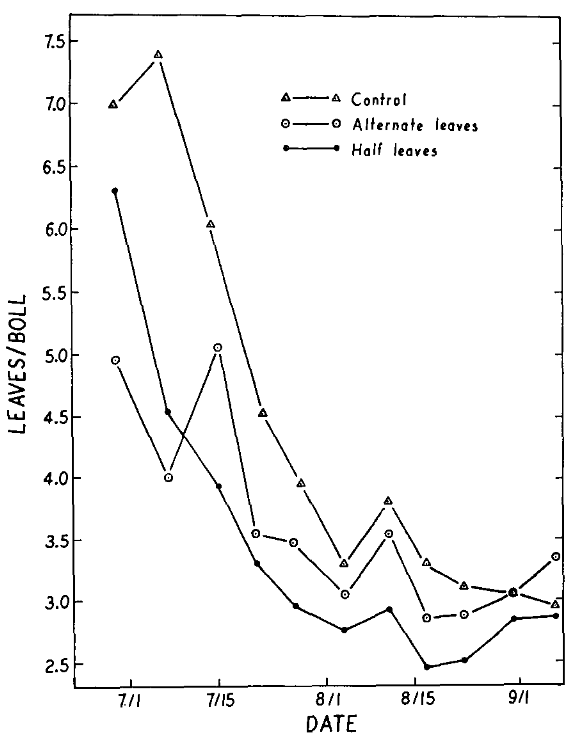


**Fig. 3. Leaf-boll ratios of control and partially defoliated plants. Mean leaf size of the treated plants was adjusted to that of control plants before calculating ratios.**

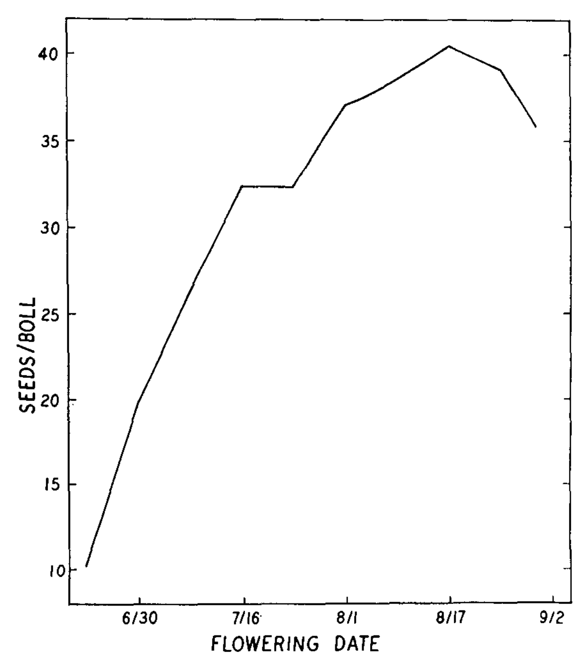


**Fig. 4. Seeds per retained boll of control plants throughout the flowering period. Means are based on bolls retained during successive 8-day periods.**

strated, with beans, that GA enhances the ability of auxin (indoleacetic acid) to attract labeled metabolites to the site of application (defruited peduncles). Treatment of all the flowers or bolls might eliminate such an advantage, so that retention would be similar to that on control plants.

The data relating retention to leaf-boll ratios indicates the importance of assimilate availability in limiting retention. Presumably, more assimilate was available at high ratios, as only a few bolls were developing. As an increasing number of bolls were undergoing development, demand for assimilate increased to the extent that availability became a factor limiting retention. Perhaps of greater significance than percent retention *per se* is the relatively constant ratio of leaves to bolls during the latter part of the fruiting period.

The slightly lower leaf-boll ratios obtained with the partially defoliated treatments can be attributed to the better light relations resulting from less self shading. No interplant competition for sunlight occurred in this experiment, but there was shading of lower leaves by upper leaves. Eaton and Ergle (8), working with field-grown plants and using a measure termed "relative fruitfulness" (no. bolls/100 g fresh wt), found slightly higher values for partially defoliated plants as compared to nontreated plants. They attributed this result to better light penetration.

That leaf area imposes limitations on productivity (retention) is further demonstrated by the data shown in the last column of Table 1. Although there were significant differences in maximum leaf area and seed cotton yield among some treatments, no differences were found when yield was expressed as a function of maximum leaf area.

Support for the view that retention is regulated by the interaction of hormonal factors emanating from the developing seed, and by assimilate availability, can be derived from consideration of the data for seeds per retained boll (Fig. 4). Early in the fruiting period few bolls were developing, and bolls with a low seed complement were able to mobilize sufficient nutrients (2) to continue growth. Presumably, as increasing numbers of bolls were developing, only those with a high seed complement were able to mobilize sufficient nutrients for continued growth, whereas bolls with a low seed complement were shed. Confirmation of this point requires further study, as it is not known what the seed complement was of the bolls that were shed.

The decline in seed index (g per 100 seeds) is a further indication that competition for assimilates increased as more bolls were retained. In this experiment, seed index for the earliest bolls set was 15.75, decreasing almost linearly to 12.40 for the last bolls. Factors such as declining light flux, daylength, and temperature very probably were responsible for the lower seed weight of the last bolls set. However, such factors should not have influenced seed weight of bolls set in mid-season; yet those seeds were lighter than seeds from the earliest bolls.

These results indicate the importance for boll retention of assimilate availability, particularly as dependent on the vegetative-reproductive status of the plant. The data for number of seeds per boll support the view that developing seeds produce growth promoting substances, and that these substances act to mobilize assimilates to the fruit.

In view of the relationship between leaf area and productivity, interpretation of data from field studies would be facilitated by information on rate and amount of leaf area development. Too frequently leaf area measurements are not taken during the conduct of agronomic studies with cotton.

## LITERATURE CITED


1. Ashley, D. A., B. D. Doss, and O. L. Bennett. 1963. A method of determining leaf area in cotton. Agron. J. 55:584-585.
2. Crane, J. C. 1964. Growth substances in fruit setting and development. Ann. Rev. Plant Physiol. 15:303-326.
3. Dale, J. E., and G. F. Milford. 1965. The role of endogenous growth substances in the fruiting of Upland cotton. New Phytol. 64:28-37.
4. Dransfield, M. 1961. Some effects of gibberellic acid on cotton. Emp. Cotton Grow. Rev. 38:3-17.
5. Dunlap, A. A. 1945. Fruiting and shedding of cotton in relation to light and other limiting factors. Texas Agr. Exp. Sta. Bull. 677.
6. Eaton, F. M. 1955. Physiology of the cotton plant. Ann. Rev. Plant Physiol. 6:299-328.
7. ————, and D. R. Ergle. 1953. Relationship of seasonal trends in carbohydrate and nitrogen levels and the effects of girdling and spraying with sucrose and urea to the nutritional interpretation of boll shedding in cotton. Plant Physiol. 28:503-520.
8. ————, and ————. 1954. Effects of shade and partial defoliation on carbohydrate levels and the growth, fruiting and fiber properties of cotton plants. Plant Physiol. 29:39-49.
9. Hall, W. C. 1958. Physiology and biochemistry of abscission in the cotton plant. Texas Agr. Exp Sta. Misc. Pub. 285.
10. Hawkins, R. S., R. L. Matlock, and C. Hobart. 1933. Physiological factors affecting the fruiting of cotton with special reference to boll shedding. Arizona Agr. Exp. Sta. Tech. Bull. 46.
11. Mason, T. G. 1922. Growth and abscission in Sea Island cotton. Ann. Bot. 36:457-484.
12. Seth, A. K., and P. F. Wareing. 1967. Hormone-directed transport of metabolites and its possible roll in plant senescence. J. Exper. Bot. 18:65-77.
13. Wadleigh, C. H. 1944. Growth status of the cotton plant as influenced by the supply of nitrogen. Arkansas Agr. Exp. Sta. Bull. 446.
14. Walhood, V. T. 1957. The effect of gibberellins on boll retention and cut-out in cotton. Proc. Cotton Defol. Physiol. Conf., 12th. 24-30. National Cotton Council, Memphis, Tenn.