

Fruiting of Cotton. III. Nutritional Stress and Cutout¹

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ABSTRACT

Decreases in growth, flowering, and fruit (boll) retention of cotton (*Gossypium hirsutum* L.) occur during the season in many modern cultivars even though it is an indeterminate plant. If they are pronounced, these decreases are commonly referred to as cutout. If cutout occurs too early it may decrease yield. Conversely, complete and permanent cutout at the end of the season would facilitate the control of insect pests. Cutout is strongly affected by boll load and may occur because of competition for photosynthate, a change in hormonal status, or both. Previous results indicated that changes in free abscisic acid (ABA) did not correlate with the decreases in growth, flowering, and boll retention that occurred as boll load increased during the season. Therefore, experiments were conducted in the field to test the hypothesis that cutout occurs when the demand for photosynthate exceeds the supply. The supply of photosynthate per plant was manipulated by thinning the plant population at different times to permit better light penetration (irradiance) into the canopy and thus increase total photosynthesis per plant. The demand for photosynthate was manipulated by partial defruiting. All flowers were removed during the first 3 weeks of flowering. Thinning at the start of the season caused individual plants to produce more flowers and bolls, but did not alter the timing of changes in flower production and boll retention rates during the season. Carrying capacity per plant varied inversely with plant population. Thinning later in the season caused an immediate increase in boll retention and a subsequent increase in flowering rate. Decreasing the demand by removing flowers early in the season caused subsequent and rather prolonged increases in flowering and boll retention rates. Early defruiting also moderated the decline in growth rate late in the season. Decreases and subsequent increases in flowering rate lagged behind the changes in growth and boll retention because flowering rate was determined by prior events (production and retention of flower buds). The results are consistent with the hypothesis that growth, flowering, and boll retention decrease when the demand for photosynthate increases and exceeds the supply. Therefore, an increase in photosynthesis should permit more bolls to be set before cutout.

Additional index words: Abscission, Active boll load, Boll retention, Competition, Flowering, Growth, Organic nutrients, Photosynthesis, Plant population.

ALTHOUGH cotton (*Gossypium hirsutum* L.) is an indeterminate plant, most cultivars exhibit cycles of growth, flowering, and fruit (boll) retention. All three activities are high early in the reproductive phase but usually decrease with increasing fruit load. Pronounced decreases in growth, flowering, and boll retention are commonly referred to as cutout (Pat-

erson et al., 1978). If cutout occurs before the end of the growing season, yield may be below what it would have been if the crop had utilized the entire growing season. Conversely, cutout at the end of the season is desirable because it facilitates harvest and deprives insect pests of a food source before they enter diapause (Kittcock et al., 1973). Therefore, it is important to learn why cutout occurs in cotton plants.

Causes of cutout have been suggested, but are not completely understood. Fruit load appears to be a major factor; as plants become loaded with bolls, growth and flowering rates slow and boll retention decreases (Ehlig and LeMert, 1973; Patterson et al., 1978). These effects could result from competition for photosynthate, a change in hormonal status, or both. If cutout is regulated by the balance of plant hormones, it may be possible to delay or hasten cutout by altering the hormonal balance. On the other hand, if cutout occurs when the demand for photosynthate exceeds the supply, altering the hormonal balance may have little effect in delaying cutout unless the supply of photosynthate is increased.

Baker et al. (1983) developed a computer simulation model in which fruit retention and the rate of plant development (e.g., production of fruiting sites) are regulated by the supply:demand ratios for carbohydrate and nitrogen. They postulated that these ratios affect hormonal balance, but cited no evidence. My results (Guinn, 1976, 1982) indicate that a nutritional stress increases boll shedding (an important aspect of cutout) through an increase in ethylene production; however, those results do not provide an explanation for other aspects of cutout (decreased growth and flowering).

Abscisic acid has characteristics that might be expected of a growth regulator responsible for cutout. It inhibits nucleic acid and protein synthesis, inhibits growth, and promotes dormancy of buds (Addicott and Lyon, 1969; Milborrow, 1974). Eaton and Ergle (1953) suggested that "boll shedding is controlled by

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the balance between auxin produced in the leaves and an anti-auxin or inhibitory material from developing bolls that is moved out into the fruiting branches." The subsequent isolation and identification of ABA from cotton bolls provided support for their suggestion (Addicott et al., 1964). Although bolls contain a relatively high concentration of ABA, results of a recent study did not support the hypothesis that bolls are a source of ABA for fruiting branches and growing points (Guinn, 1984). The ABA concentration in fruiting branches and stem apices did not increase with boll load as cutout was approached, and was not altered by partial defruiting. Therefore, it seemed necessary to evaluate other hypotheses.

The experiments reported in this paper were conducted to test the hypothesis that cutout is caused by an imbalance between demand for and supply of photosynthate. Specifically, the hypothesis states that an increase in demand for photosynthate by an increasing boll load causes the decreases in growth, flowering, and boll retention that we refer to as cutout. The balance between supply and demand was manipulated by increasing the supply and by decreasing the demand. The results were consistent with the hypothesis.

MATERIALS AND METHODS

An experiment was conducted in 1982 to investigate the effects of plant population on the boll-carrying capacity of individual plants. 'Deltapine 70' cotton seed were planted on the University of Arizona Cotton Research Station in Phoenix on 7 April after a preplant irrigation in March. The soil is an Avondale clay loam (a member of the fine-loamy, mixed, hyperthermic family of Typic Torrifluvents). Nitrogen was applied as urea in equal amounts before planting and on 16 June to give a total of 155 kg of N per ha. Irrigations were applied on 27 May, 17 June, and every 2 weeks thereafter through 25 August.

Seedlings were thinned by hand to give populations of approximately 50 000, 100 000, and 200 000 plants per ha in plots that were three rows wide by 4 m long. Row spacing was about 1 m. Flowers were counted and tagged daily with dated tags on plants in the center row of each plot. The treatments were replicated four times in a randomized complete block.

The active boll load was calculated by recovering retained tags in the fall and calculating the total number of bolls from one through 45 days old that were present on a plant on a given date. Data for Saturdays and Sundays were estimated by interpolation. Bolls older than 45 days were not included, nor were bolls that abscised.

An experiment was conducted in 1983 to investigate the effects of thinning at different times on subsequent flowering and boll retention. 'Deltapine 61' cotton seed were planted on the Arizona State University Experimental Farm in Tempe on 25 April after a preplant irrigation in March. Plots were irrigated on 27 May, 20 June, and every 2 weeks thereafter through 26 August. The soil is a Contine clay loam (a member of the fine, mixed, hyperthermic Typic Haplargids).

All plots were hand-thinned in the seedling stage to approximately 99 000 plants per ha. The control plots remained at that population. Plants in the three thinning treatments were subsequently removed on 14 June, 5 July, and 26 July to give populations of about 33 000 plants per ha. These dates corresponded to first visible square, first

flower, and 3 weeks after first flower, respectively. Each plot was three rows wide by 6 m long. A 4-m segment of each center row was used for flower counting and tagging. Flowers were counted and tagged daily with dated tags after the plots were thinned. The four treatments were replicated four times in a Latin square.

A separate experiment was conducted with the same cultivar in a different part of the same field in 1983 to investigate the effects of assimilate demand (fruit load) on growth, flowering, and boll retention. Fruit load was altered by removing all flowers daily during the first 3 weeks of flowering (through 27 July) in the defruited (DF) plots. Plants in the control (C) plots were permitted to fruit normally. Each plot was 10 m long and the treatments were replicated four times in a randomized complete block.

Flowers were counted and tagged on Monday and Thursday of each week. Fruiting branches and main stems were measured on Wednesdays. A white flower at the first node of a fruiting branch was the reference point used for selecting fruiting branches and the position on the main stem from which to make the measurements. The fruiting branch was measured from the first node to the tip, and the main stem was measured from that fruiting branch to the apical growing point. Four different plants were selected in each plot each week.

Percentage boll retention was estimated by comparing numbers of tagged flowers with retained, tagged bolls at the end of the season.

RESULTS

Plant population had a pronounced effect on the number of flowers produced per plant, but did not change the timing of maximum and minimum flowering (Fig. 1) or boll retention rates (Fig. 2a,b,c). Flowering rate per plant responded to population and soon became almost inversely proportional to plant population (Fig. 1). The total flowers produced per m² of land area were 259, 283, and 309 in the low, medium, and high populations, respectively.

Active boll load had a pronounced effect on boll retention. Boll retention started decreasing almost as soon as the first bolls were set and declined to minimum values in early August (Fig. 2a,b,c). Boll retention started to increase again as soon as older bolls began to mature and the active boll load started to decrease. Because of very low flower counts during

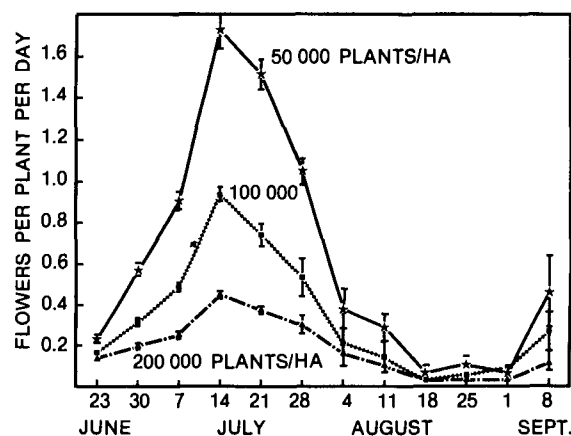


Fig. 1. Number of cotton flowers produced per plant per day during the season as influenced by plant populations of 50 000, 100 000, and 200 000 plants per ha.

the last half of August (Fig. 1) it was not possible to obtain meaningful boll retention rates during the week of 22 to 27 August, and also during the previous week in the low population (Fig. 2a). Decreases and increases in flower counts lagged behind the decreases and increases in boll retention rates. Flowering did not start increasing after cutout until the week of 6 to 11 September (Fig. 1).

High plant population greatly decreased the carrying capacity of individual plants; active boll load per plant was inversely related to plant population. Total number of bolls produced per m² during the season were 104, 114, and 117 in the low, medium, and high populations, respectively. However, bolls were smaller at the higher population. Yields from

the first two hand pickings of adjacent untagged plots averaged 5404, 5401, and 4763 kg seed cotton per ha in the low, medium, and high populations, respectively. The yield was significantly lower in the high population despite more bolls.

Thinning at different times during the season in 1983 caused pronounced increases in flowering per plant (Fig. 3a) and boll retention (Fig. 3b). For clarity, flowering rates were calculated as percentages of the control rate during each time interval and were plotted only until maximum values were reached (Fig. 3a). Flowering increased slightly immediately after thinning, possibly because of improved square retention. However, substantial increases in flowering were not evident until about 4 weeks after thinning. Flowering continued to increase in thinned plots, relative to controls, until it reached a maximum about 40 to 45 days after thinning (Fig. 3a), probably due to increased growth and production of fruiting sites. A decrease in flowering in the controls during the season emphasized the increased flowering rates in the thinned treatments, especially late in the season.

Boll retention decreased during the season (as boll load increased), but remained much higher in thinned than in control plots until late in the season (Fig. 3b).

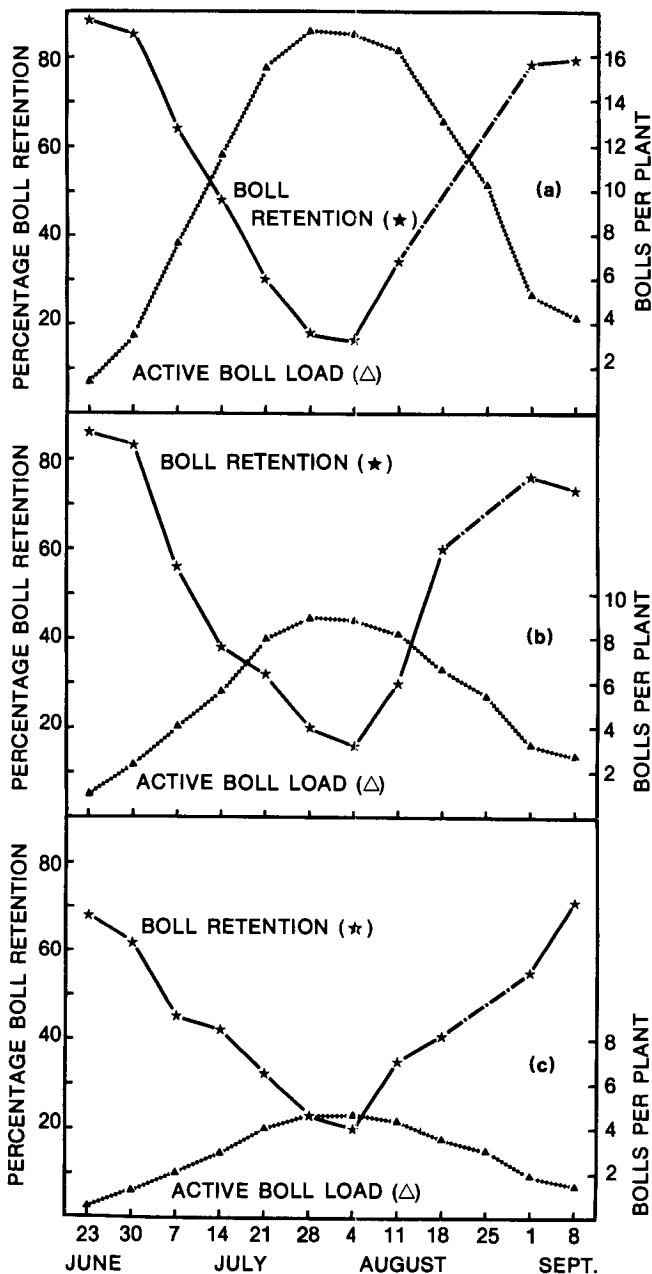


Fig. 2. Relationship between active boll load and percentage boll retention of cotton at populations of 50 000 (a), 100 000 (b), and (c) 200 000 plants per ha.

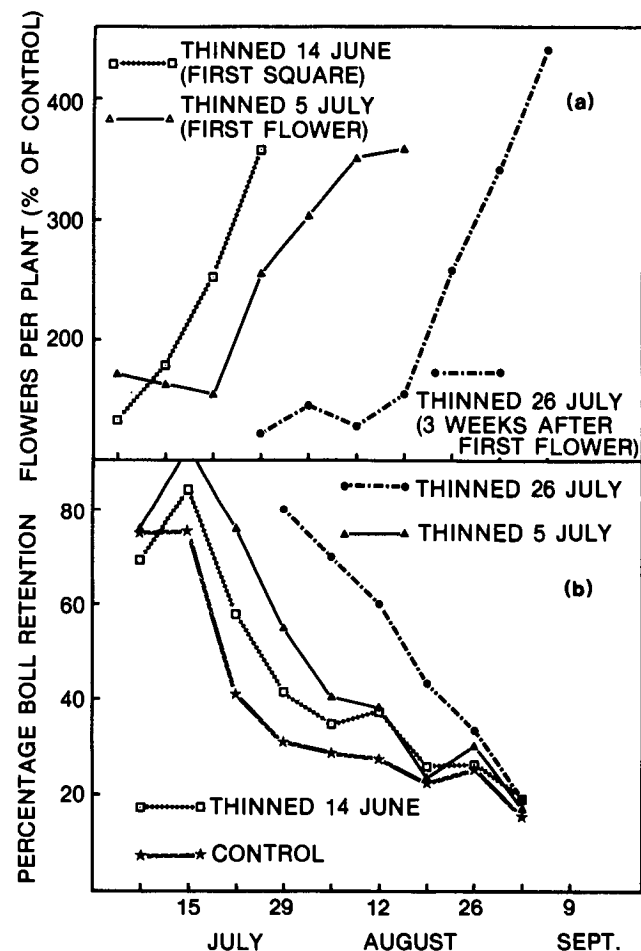


Fig. 3. Flowering of cotton plants, as a percentage of the control rate (a), and percentage boll retention (b) as influenced by removing two-thirds of the plants at first square, first flower, or 3 weeks after first flower to decrease interplant competition.

Table 1. Daily boll retention rates of control cotton plants and of plants thinned to one-third the control population on 26 July, 3 weeks after first flower.

Date	Control	Thinned
	%	
25 July	26 ± 4	—
26 July†	30 ± 11	78 ± 8
27 July	26 ± 9	64 ± 13
28 July	29 ± 5	97 ± 3
29 July	40 ± 6	83 ± 6

† Date the stand was thinned. Data are averaged of four replications ± SE.

The data in Fig. 3b were plotted as weekly averages. Daily rates were compared to see how soon boll retention increased after plants were thinned. The results indicate an immediate effect; plants that were thinned on 26 July retained more than twice the percentage of flowers that appeared that day than were retained by the unthinned controls (Table 1). Thinning probably increased the supply of photosynthate per plant by permitting higher irradiance in the lower portion of the canopy. In the next experiment, removal of early flowers altered the balance between supply of assimilates and demand for them by decreasing the demand.

Decreasing the demand (competition) for photosynthate, by removing all flowers during the first 3 weeks of flowering, caused subsequent increases in flowering (Fig. 4a) and boll retention (Fig. 4b). Early defruiting also caused flowering to continue later in the season (Fig. 4a). Growth of main stems and fruiting branches decreased greatly during the season. The early decreases in growth in DF were probably due to a stunting effect of handling the plants (Frizzel et al., 1960); considerable manipulation was required in searching for and removing all flowers daily for 3 weeks in DF. Mainstem and fruiting branch lengths decreased less in DF than in C after 27 July, when flower removal was discontinued (Table 2). Therefore, all three parameters of cutout — growth, flowering, and boll retention — were affected when demand for photosynthate was decreased.

DISCUSSION

Cutout is a process rather than an abrupt event. All three parameters of cutout (growth, flowering, and boll retention) decreased gradually during the season; they did not stop abruptly. However, changes in flowering rate lagged behind changes in growth and boll retention because flowering is a secondary response that depends upon the earlier events of growth (and the associated production of fruiting sites) and the retention of flower buds (squares). New growth occurred at least 3 weeks before flowering rate increased after cutout. Likewise, percentage boll retention started increasing about a month before the recovery in flowering. Because of the delayed response, flowering rate is not an accurate indicator of current plant status in relation to cutout. However, an early increase in boll retention is of little practical importance as long as the flowering rate remains low.

The significant effect of boll load on boll retention has been noted by others (e.g., Tugwell and Waddle, 1964), but most workers did not differentiate be-

Table 2. Length of main stem and a fruiting branch of cotton plants in relation to boll load during the season in control (C) and partially defruited (DF) plants.†

Date	Length				Boll load	
	Main stem		Fruiting branch			
	C	DF	C	DF	C	DF
	mm				bolls/m ²	
6 July	432 ± 9	—	214 ± 11	—	0.6 ± 0.2	0
13 July	359 ± 19	304 ± 21	187 ± 12	162 ± 18	10.3 ± 1.8	0
20 July	224 ± 15	148 ± 7	162 ± 11	104 ± 6	28.3 ± 4.1	0
27 July	150 ± 14	131 ± 5	113 ± 4	111 ± 12	33.8 ± 5.5	0
3 August	70 ± 18	105 ± 9	45 ± 12	80 ± 10	55.4 ± 6.8	39.8 ± 1.9
10 August	40 ± 8	77 ± 5	39 ± 11	80 ± 8	63.9 ± 6.6	57.5 ± 1.9

† The mainstem was measured from the apex to a fruiting branch with a white flower at the first node of the fruiting branch. The fruiting branch with a white flower at the first node was measured from the first node to the branch tip. Data are averages of four replications ± SE.

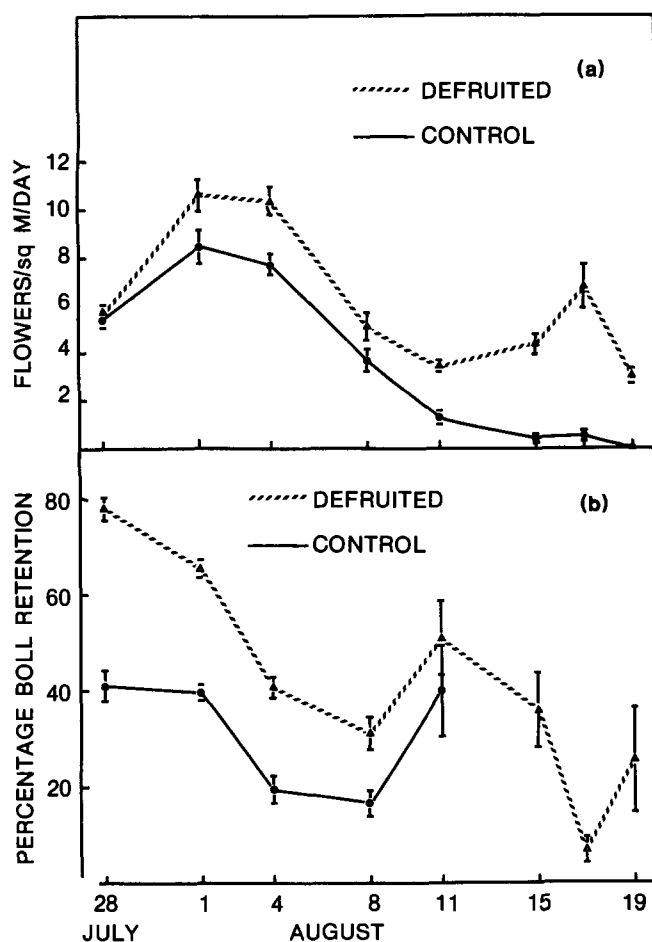


Fig. 4. Flowering rate of cotton plants (a) and percentage boll retention (b) through the season as influenced by removing all flowers during the first 3 weeks of flowering (through 27 July). Vertical bars indicate standard errors of the means.

tween total boll load and “active” boll load. The concept of active boll load was introduced earlier (Guinn and Mauney, 1984) and is based on the assumption that bolls are part of the active boll load only as long as they compete for assimilate. As bolls approach maturity their growth and respiration rates decline to very low levels (Mutsaers, 1976). If bolls affect cutout because of their competition for assimilate, mature bolls would have no effect and should not be included as part of the active boll load. The fact that boll

retention rate increased as soon as active boll load started decreasing (Figs. 2a,b,c) fits the hypothesis that bolls influence cutout because of their competition for assimilate.

For simplicity, only bolls that were between 1 and 45 days old were considered as part of the active boll load. No attempt was made to assign different demand functions to different aged bolls within that age bracket, nor to adjust demand and physiological boll ages according to temperature.

Kerby and Buxton (1981) determined the effects on fruit retention of competition at adjacent sites. My results indicate that the effect extends much farther. Bolls approaching 45 days old were many nodes away from young bolls that shed, but their presence apparently affected the retention of young bolls. Otherwise, why did boll retention start increasing as older bolls matured? This effect was noted at all three plant populations (Fig. 2a,b,c) and has been noted in other years (Guinn and Mauney, 1984; Guinn, unpublished data).

Previous results of Mauney et al. (1978) strongly support the hypothesis that cutout occurs when the demand for photosynthate exceeds the supply. They increased the supply of photosynthate by enriching the air with CO₂, which increased the measured rates of photosynthesis. Enrichment with CO₂ also increased growth, flowering, and boll retention, and delayed cutout by about 10 days.

In conclusion, my results and previous results of Mauney et al. (1978) are consistent with the hypothesis that a deficiency of photosynthate is a major cause of cutout (but not necessarily the only cause). Therefore, any treatment or condition that causes higher rates of photosynthesis should make it possible for the cotton plant to set more bolls before it "cuts out."

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