Spatial Yield Distribution in Cotton Following Early-Season Floral Bud Removal

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ABSTRACT

A better understanding of cotton (*Gossypium hirsutum* L.) compensatory growth after loss of early-season floral buds requires an assessment of the actual patterns of spatial yield distribution in damaged and undamaged plants. This study was conducted to determine if spatial yield distribution or yield components are altered in cotton in response to removal of early-season floral buds. Beginning with the second week of squaring, floral buds were removed by hand for one, two, or three consecutive weeks. At 90 d after planting, plant height, leaf area index, main stem node number, fruit present, total fruiting positions, and dry weights were measured. The contribution to total yield from each fruiting position was determined at crop maturity. Results from this study show the lowest level of floral bud removal resulted in no differences in spatial yield distribution. As the intensity of early-season floral bud removal increased, however, the probability of harvesting a mature boll decreased in the lower canopy but increased in the upper canopy. Removal of floral buds resulted in fewer first sympodial position fruit but more third sympodial position fruit at harvest. Thus, early-season removal of floral buds resulted in additional seed cotton production on more apical and distal fruiting positions. These modifications in spatial yield distribution adequately replaced those floral buds removed early in the season because total seed cotton yield was not different among the treatments at crop maturity.

Across much of the U.S. cotton belt, broad-spectrum insecticides are applied early in the growing season to protect fruiting forms from insect pests such as the boll weevil (*Anthonomus grandis grandis* Boheman) and the tobacco budworm [*Heliothis virescens* (Fabricius)] (Mann et al., 1997). These applications not only increase production costs and environmental contamination, but also increase the likelihood of insecticide resistance development (Plapp et al., 1990) and decrease the populations of beneficial arthropods (House et al., 1985). In the southeastern region of the U.S. Cotton Belt, the Boll Weevil Eradication Program has virtually eliminated *A. grandis* as an economic insect pest. In addition, cotton cultivars that contain genes for expression of the delta-endotoxin of *Bacillus thuringiensis* (Bt) are becoming widely accepted. These technological advances have resulted in a decline in insecticide use against *A. grandis* and *H. virescens* (Mann et al., 1997). Boll weevil eradication and Bt cotton are cornerstones of current integrated pest management (IPM) systems for cotton. One addition that may strengthen cotton IPM systems and lessen the dependence on insecticides is potential for compensatory growth following early-season floral bud loss due to insects.

In cotton, economic thresholds in pest control decisions are based on several factors, including insect densities, cultivar/technology utilization, weather, equipment, and farm size (Mi et al., 1998). Economic thresholds, however, rarely consider plant compensation for loss of early-season floral buds as part of the model. Inclusion of plant compensation in economic injury levels would raise treatment thresholds, thereby reducing insecticide applications and the costs, contamination, and resistance development related to them. Prior to inclusion in an economic injury level, however, the ability of cotton to compensate for loss of early-season floral buds must be fully documented.

Many studies have investigated the ability of cotton to compensate for loss of fruiting forms with results that have ranged from small increases to large decreases in final lint yield (Sadras, 1995). In a review of the literature, Sadras (1995) indicated a better understanding of compensatory growth after loss of floral buds requires characterization of the actual patterns of spatial yield distribution in damaged and undamaged plants. Until now, no study has been conducted to determine if spatial yield distribution in cotton is altered by loss of early-season floral buds. Spatial distribution analyses of final lint yield will more fully determine if and how cotton plants may compensate for loss of early-season floral buds.

In describing plant compensation to loss of floral buds, Sadras (1995) further developed four types of responses that were originally defined by Hearn and Room (1979), Kletter and Wallach (1982), and Brook et al. (1992). First is a passive and instantaneous response in which reproductive structures that are damaged by insects would have shed physiologically anyway, resulting in no observable change in the spatial distribution of lint yield. Second is a passive and time-dependent response in which other reproductive structures that would have shed physiologically are retained, replacing those lost to insect damage. Third is an active and instantaneous response in which resources that would have been partitioned into damaged structures are partitioned into undamaged ones, resulting in increased boll weight. Fourth is an active and time-dependant response in which resources that would have been partitioned into damaged structures are partitioned into the production of additional fruiting sites, resulting in delayed crop maturity. The method in which cotton may compensate for loss of early-season floral buds, however, may be a combination of all possible responses.

The objectives of this investigation were to determine

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Abbreviations: Bt, *Bacillus thuringiensis*; CPES, Coastal Plain Experiment Station; CPES'99, 1999 study at the Coastal Plain Experiment Station Ponder Farm; IPM, integrated pest management; LAI, leaf area index; NACB, nodes above cracked boll; RDC'98, 1998 study at the Coastal Plain Experiment Station Rural Development Center Farm; RDC'99, 1999 study at the Coastal Plain Experiment Station Rural Development Center Farm.

(i) if spatial distribution of lint yield is altered in cotton in response to loss of early-season floral buds, and (ii) which of the mechanisms outlined by Sadras (1995) are utilized in the redistribution of lint yield. We propose redistribution of lint yield in response to loss of early-season floral buds is possible and the mechanism of redistribution is most likely a combination of those proposed by Sadras (1995).

MATERIALS AND METHODS

Cultural Practices

Studies were conducted at one location in 1998, and two locations in 1999. The 1998 study was conducted at the Coastal Plain Experiment Station (CPES) Rural Development Center Farm (RDC'98). The study was repeated in 1999 at the CPES Rural Development Center Farm (RDC'99) and the CPES Ponder Farm (CPES '99). Both locations are in Tift County, GA, on a Tifton loamy sand (Fine-loamy, kaolinitic, thermic Plinthic Kandiudults).

Cotton, 'DeltaPine 33b' was planted on 30 April (RDC'98) 1998, and 3 May (RDC'99) and 10 May (CPES'99) 1999 with a Monosem air planter (Lenexa, KS) on 91-cm row widths at a seeding rate of 10.8 seeds m^{-2}. While planting, 5.7 kg ha^{-1} Aldicarb [2-methyl-2-(methylthio) propionaldehyde O-(methylcarbamoyl)oxime] was applied in furrow for insect control. Fertility, weed control, and insect scouting and control measures in all studies were in accordance with the University of Georgia Cooperative Extension Service guidelines (Brown et al., 1998). Water stress was minimized with sprinkler irrigation in all studies. Harvest aids were applied (2.3 L ha^{-1} of ethephon plus cyclanilide and 0.07 kg ai ha^{-1} of thidiazuron) in mid-September in all studies. The experimental design used in all studies was a randomized block design with three (RDC'98 and RDC'99) or four (CPES'99) replicates. Each plot was 4 rows wide and 15 m long.

Treatment Establishment

Hand removal of floral buds began early during the second week of squaring (≈43 d after planting) in each study. Only floral buds that were match-head size or larger (i.e., ≥3 mm) were removed in order to prevent damage to meristematic regions. During removal, floral buds that met the size criteria were grasped between the index finger and thumb and twisted until the peduncle snapped and the floral bud became disjoined. The treatments were as follows: (i) 50% floral bud removal for 1 wk, (ii) 100% floral bud removal for 1 wk, (iii) 50% floral bud removal for two consecutive weeks, (iv) 100% floral bud removal for two consecutive weeks, (v) 50% floral bud removal for three consecutive weeks, (vi) 100% floral bud removal for three consecutive weeks, and (vii) untreated. All floral buds on a sympodial branch that met the size criteria, regardless of position, were considered for removal. For the 50% floral bud removal treatments, all floral buds that met the size criteria were counted on a single plant, and one-half of these floral buds were removed at random. During the first week of removal, floral buds were removed from the first two-to-three sympodial branches. Most of the floral buds that were removed during this week were from first sympodial positions, as floral buds from second sympodial positions had not met the size criteria. Sympodial positions greater than two were not present at this time. During the second week of removal, floral buds were removed from the first four-to-five sympodial branches. Most of the floral buds that were removed during this week were from first and second sympodial positions, as floral buds from third sympodial positions had not met the size criteria. During the third week of removal, floral buds were removed from the first six-to-seven sympodial branches. Most of the floral buds that were removed during this week were also from first and second sympodial positions, as floral buds from third sympodial positions that met the size criteria had only been produced on the first one or two sympodial branches. During each week of floral bud removal, an additional one-to-two sympodial branches were noted in the apex of each plant. Floral buds were not removed from these branches, as they had not met the size criteria. One of the two center rows of each plot was randomly chosen for hand removal of floral buds. Floral buds were removed from the entire 15 m of the chosen row in each plot.

Data Collection

Growth analyses were conducted 90 d after planting in each study (during the boll-filling stage). For each growth analysis, all plants from 1 m of row in each plot were cut at the soil level, hand defoliated, and total leaf area was determined with an area meter (model LI-3100, LI-COR, Lincoln, NE). Plant height and total number of main stem nodes were then determined on each plant following leaf area determination. Next, the total number of squares, bolls, and missing positions were counted. Finally, dry weights of stems, leaves, squares, and bolls from each plot were determined after drying to uniformity at 60°C.

During the 3 wk prior to crop maturity in 1999, nodes above cracked boll (NACB) were counted on 6 different d in both studies. For this determination, the number of main stem nodes from the uppermost first sympodial position cracked boll to the uppermost harvestable boll were counted on ten plants in each plot. A harvestable boll was defined as a boll that had achieved full size (i.e., at least 3 wk old).

At harvest, 3 m of row in each plot were hand harvested as described by Jenkins et al. (1990a). Seedcotton, boll number, and boll weight at each fruiting site was documented. Thus, the contribution to total yield was determined for each fruiting position. All cotton on monopodial branches was harvested as one position. The only change in the Jenkins et al. (1990a) methodology was the cotyledonary node was counted as Node 0. In this investigation, every effort was made to establish the treatments accurately as outlined in the protocol. When the protocol required 100% floral bud removal, we attempted to remove precisely 100% of the floral buds that met the size criteria. Hand-harvest data collected at season's end, however, indicated that we were 85 to 90% efficient in our attempts to remove floral buds.

Statistical Analyses

Analysis of the Data Collected During the In-Season Growth Analyses and Data Collected from Monopodial Fruiting Positions at Harvest

A split plot in time (Steel and Torrie, 1980) was used to analyze the data. Study areas were considered main plots (two fields that were spatially separated were used in the two study years), blocks within study area as subplots, and treatments as sub-subplots. The Proc Mixed procedure (Littell et al., 1996) was used to analyze the data. The initial model considered study area and blocks within study area as random effects, while treatments were fixed effects. The second model analyzed six of the seven treatments as a two-by-three factorial consisting of two rates of floral bud removal and three times. A third analysis examined the linear and quadratic effects of time within levels of floral bud removal.

Analysis of the Data Collected from Sympodial Fruiting Positions at Harvest

The same model as before was used for analysis of these data, with the addition of nodes as sub-sub-subplots. Additional random error terms were blocks by treatments within study areas and blocks by nodes within study areas. Additional fixed effects were nodes and treatment by node interactions. The second model used six of the treatments as a two-by-three factorial as previously described. The third model examined the linear and quadratic effects of time and their interactions with level of floral bud removal and node.

Analysis of the Nodes Above Cracked Boll Data Collected Immediately Prior to Harvest

The same model as before was used for analysis of these data with the addition of dates as sub-sub-subplots and data from ten plants sampled at random as within sampling units. Additional random error terms were blocks by treatments within study areas, blocks by dates within study areas, and blocks by treatments by dates within study areas. Additional fixed effects were dates and treatment by date interactions. The second model used six of the treatments as a two-by-three factorial, as previously described. The third model examined the linear and quadratic effects of time and date and their interactions and interactions with level of floral bud removal.

RESULTS AND DISCUSSION

Growth Analyses

Sadras (1995) indicated that fruit loss changes partitioning of plant resources in favor of vegetative structures. This shift in partitioning increases the ability of the crop to acquire carbon and nitrogen and potentially increases the crop compensation capacity. Several studies have shown increased plant height (Patterson et al., 1978; Kennedy et al., 1986, 1991; Pettigrew et al., 1992; Holman and Oosterhuis, 1999) and leaf area index (LAI; Kennedy et al., 1986; Jones et al., 1996b) as a result of fruit loss. Our data (Table 1) illustrate that plant height and LAI were as much as 6 and 9% greater, respectively, 90 d after planting when early-season floral buds were removed. Additionally, the number of main stem nodes per plant 90 d after planting increased with duration of floral bud removal in our studies (Table 1). These data are in agreement with Kennedy et al. (1986), who reported an increased number of sympodia per plant with floral bud removal.

One of the proposed mechanisms of plant compensation for loss of early-season floral buds occurs through the production of additional fruiting sites (Sadras, 1995). Our data (Table 1) show that total fruiting positions (retained positions plus aborted/removed positions) and fruit present 90 d after planting increased with duration of floral bud removal. Kennedy et al. (1991) and Malik et al. (1981) also reported increased production of fruiting sites with floral bud removal, while Jones et al. (1996b) and Ungar et al. (1987) reported increased production of fruiting forms with early-season fruit removal. In the current study, however, the increase in number of fruiting positions and total number of fruit present did not change the percentage of fruit retained by the crop 90 d after planting [(total fruit present/total fruiting positions) $\times$ 100] (Table 1). Percentage retention 90 d after planting ranged from 57.9 to 59.2, and was not significantly different among treatments.

Jones et al. (1996b) and Pettigrew et al. (1992) reported that fruit removal decreased the reproductive: vegetative ratio during the boll filling stage of crop development. Our data also show a decreased fruit:shoot ratio (fruit dry weight per unit shoot dry weight) 90 d after planting with floral bud removal (Table 1). This is primarily attributed to the greater number of floral buds present (relative to bolls) with floral bud removal when the sampling was conducted. The percentage of bolls [(total bolls present/total fruit present) $\times$ 100] 90 d after planting ranged from 75.0% in the untreated to 52.5% in the most severe floral bud removal treatment (Table 1). While these data were collected 90 d after planting, they indicate that a delay in crop maturity is likely.

Numerous studies have demonstrated delayed crop maturity in response to fruit removal (McCarty et al., 1986; Ungar et al., 1987; Kennedy et al., 1991; Brook et al., 1992; Pettigrew et al., 1992; Jones et al., 1996b; Mann et al., 1997; Holman and Oosterhuis, 1999). Brook et al. (1992) and Mann et al. (1997), however, reported that maturity was delayed only by the greatest levels of

Table 1. Plant height, leaf area index (LAI), number of mainstem nodes, total number of fruiting positions, fruit present, percent retention, fruit:shoot ratio, and percent bolls at 90 d after planting in fruit removal studies conducted at Tifton, GA, in 1998 and 1999.

Treatment	N	Plant height	LAI	Mainstem nodes	Total positions	Fruit	Retention	Fruit:shoot	Bolls
		cm plant^{-1}	m^{-2}	plant^{-1}	m^{-2}		%	g^{-1}	%
wk of fruit removal									
0	10	101.8b†	4.0b	19.0b	338c	200c	59.2a	0.37a	75.0a
1	20	105.4ab	4.1ab	19.3ab	366bc	212bc	57.9a	0.33a	70.2a
2	20	108.0a	4.4a	20.2a	397ab	231ab	58.2a	0.25b	59.6b
3	20	108.3a	4.4a	20.3a	427a	251a	58.8a	0.22b	52.5b
ANOVA									
Source of variation									
Percent removal (R)		NS‡	NS	NS	NS	NS	NS	NS	NS
Weeks (W)		*	*	**	**	**	NS	**	*
R $\times$ W		NS	NS	NS	NS	NS	NS	NS	NS
df		54	54	42	54	54	12	42	42
LSD (0.05)		5.75	0.38	0.87	34	24	4.0	0.05	7.4

* Significant at $P = 0.05$.
** Significant at $P = 0.01$.
† Means followed by the same letter within a column are not significantly different ($P = 0.05$). Least square means are presented.
‡ NS = not significant.

fruit loss. Mann et al. (1997) also reported that the levels of fruit loss that delayed maturity in their studies are seldom encountered in the field. Crop maturity in our studies, as determined by NACB counts, was not different during the 3-wk period prior to harvest-aid application (Table 2). If a cotton crop may be considered mature at NACB $\leq$ 5 (Brown et al., 1998), however, then crop maturity in the untreated control occurred at 127 d after planting, while crop maturity in the treated plots was delayed from 3 to 7 d (Table 2). Interestingly, in some treatments floral buds were removed for three consecutive weeks, but crop maturity in these treatments was delayed for only 1 wk. This discrepancy may be partially explained by the greater LAI at 90 d after planting in the treated plots (Table 1). The greater LAI may have increased the ability of the crop to acquire carbon (Sadras, 1995), resulting in an increased rate of boll development and small differences in crop maturity at the season's end. Also, Malik et al. (1981) reported that vegetative organs provide efficient storage for excess assimilates, resulting from the complete suppression of early-season fruiting activity. Given that the rate of canopy photosynthesis in cotton declines beginning at ≈80 d after planting (Peng and Krieg, 1991), storage of excess assimilates prior to anthesis may provide additional carbohydrates for boll filling later in the growing season.

Yield Distribution

Several researchers have reported increased boll weight with removal of early-season floral buds (Kletter and Wallach, 1982; Brook et al., 1992; Pettigrew et al., 1992; Jones et al., 1996a). Kerby and Buxton (1981) showed that developing fruiting forms compete for carbohydrates. Thus, fruit removal in these studies may have increased the amount of carbohydrate available for developing bolls. While considerable variability exists in our data, they show that early-season floral bud removal tends to decrease first position boll weight (Table 3). Across all studies, first position boll weight was greatest with the untreated and the lowest levels of floral bud removal (i.e., 50% removal for one and two consecutive weeks). Conversely, boll weight was least with the most

Table 2. Nodes above the uppermost first position cracked boll (NACB) at 6 different d after planting (DAP) in fruit removal studies conducted at Tifton, GA, in 1999.

Treatment		N	DAP					
			120	124	127	130	134	138
% removal	wk		NACB					
0	0	70	5.8†	5.6	4.9	4.8	3.1	1.6
50	1	70	7.3	6.8	6.1	5.9	4.1	3.0
50	2	70	7.4	6.1	5.6	5.1	3.8	2.0
50	3	70	7.2	6.5	5.6	4.8	3.6	2.7
100	1	70	7.0	6.1	4.8	4.4	3.4	1.8
100	2	70	7.2	7.1	6.1	5.7	4.2	2.9
100	3	70	7.6	7.3	5.8	5.5	4.1	2.8
DAP Mean‡		490	6.9a	6.4b	5.5c	5.1c	3.7d	2.3e
LSD (0.05 = 0.43)								

† Analyzed as a split plot in time with subsampling. Percentage removal, weeks, percentage removal × weeks and their interactions with DAP were not significant ($P = 0.05$).

‡ Means followed by the same letter are not significantly different.

intense levels of floral bud removal. Jenkins et al. (1990b) showed first sympodial position boll weight increases from main stem Nodes 6 to 12 and decreases from main stem Node 12 to the plant apex. In our studies, fruit arising on main stem Nodes 6 to 12 were practically eliminated in the most intense floral bud removal treatments. We conclude that, averaged across main stem nodes, first position boll weight in our studies decreased in response to intense floral bud removal because the largest fruit normally produced by the plant (i.e., first sympodial position fruit at main stem Nodes 6–12) were removed as floral buds. Fruit arising on second and third sympodial positions, however, did not follow the same trend. Averaged across main stem nodes, second and third sympodial position boll weights and the average boll weight were not different from the control (Table 3). These data indicate that first sympodial position boll weights above main stem Node 12 will never be as great on those occurring below main stem Node 12, even if the bolls below main stem Node 12 are absent. Additionally, the resources that would have gone into bolls produced below main stem Node 12 apparently were not utilized for the production of heavier second and third sympodial positions. Thus, our data do not support the hypothesis outlined by Sadras (1995) that plant compensation for loss of early-season floral buds occurs through the production of heavier fruits. Finally, Jones et al. (1996a) reported loss of late-season flowers appeared to increase boll weight more than loss of early-season flowers. Therefore, because of differences in crop developmental stage or growing season limitations after damage, compensation for loss of early-season fruiting forms may occur more through the production of additional fruiting sites, while compensation for loss of late-season fruiting forms may occur more through the production of heavier fruit.

Brook et al. (1992) and Kletter and Wallach (1982) reported that cotton compensates for loss of early-season fruiting forms through increased boll retention. Our results (Table 4) show that the number of harvestable bolls in the first sympodial position decreased with increasing early-season floral bud removal. Averaged across main stem nodes, the probability of harvesting a mature boll in the first sympodial position was greatest in the untreated (31.9%) and 50% floral bud removal for 1-wk treatment (31.9%), and lowest in the 50 and 100% floral bud removal for 3 wk treatments (24.4 and 21.6%, respectively). In the second sympodial position, no treatment was different from the untreated. In the third sympodial position, however, the results were opposite from those found in the first sympodial position. Averaged across main stem nodes, the probability of harvesting a mature boll in the third sympodial position was greatest in the 50 and 100% floral bud removal for 3 wk treatments (8.8 and 11.9%, respectively) and lowest in the untreated (4.8%) and 50% floral bud removal for 1-wk treatment (5.5%). These results are similar to Jones et al. (1996b), who found that flowers lost during anthesis were adequately replaced by more distal fruit. Totaled across sympodial positions, the probability of harvesting a mature boll was lesser in the most intense

Table 3. Boll weight at harvest on cotton plant sympodia and monopodia in fruit removal (FR) studies conducted at Tifton, GA, in 1998 and 1999.

Treatment	N	1	N	2	N	≥3	N	Monopodia	N	Average
	Sympodial position									
	g seedcotton boll^{-1}									
100% FR 1 wk	167	4.20b†	143	3.95ab	105	3.54a	1	3.87ab	416	3.95ab
100% FR 2 wk	165	3.80d	145	3.83bc	120	3.52a	1	3.90ab	4.31	3.73b
100% FR 3 wk	155	4.09bc	139	4.08a	125	3.72a	1	3.94ab	420	3.98ab
50% FR 1 wk	175	4.22ab	147	3.71c	107	3.54a	1	3.60b	430	3.88ab
50% FR 2 wk	165	4.41a	145	4.05ab	103	3.83a	1	4.01a	414	4.14a
50% FR 3 wk	168	3.98cd	148	3.84bc	110	3.53a	1	3.95ab	427	3.82b
Untreated	174	4.23ab	143	3.91abc	89	3.61a	1	4.01a	407	3.98ab
						ANOVA				
Source of variation										
Treatment (T)		*		*		*		*		*
Node (N)		**		**		**		NA		NA
T × N		**		NS‡		NS		NA		NA
df		54		54		54		54		54
LSD (0.05)		0.187		0.229		0.372		0.380		0.261

* Significant at $P = 0.05$.
** Significant at $P = 0.01$.
† Means followed by the same letter within a column are not significantly different ($P = 0.05$). Least square means are presented.
‡ NS = not significant.

floral bud removal treatments (i.e., 50 and 100% floral bud removal for three consecutive weeks). No other treatment was different from the untreated. Thus, our results may not support the hypothesis outlined by Sadras (1995), that cotton might compensate for loss of fruiting forms through increased fruit retention. Plotting boll retention across main stem nodes, however, presents a different picture.

Table 5 presents the regression coefficients for the probability of harvesting a mature first and third sympodial position boll. Second sympodial position data were not significant and are not presented. It should be noted for the regression analyses that the intercept was set at main stem Node 7. This was done because the slope was generally greatest at main stem Node 7 in the data collected.

Intercepts for the probability of harvesting a mature first sympodial position boll were greatest in the undamaged plants, and lowest in the most severely damaged plants (Table 5). These data illustrate that early-season floral bud removal resulted in decreased percentage boll retention in the first sympodial position at the bottom of the plant canopy (Fig. 1). The linear component, however, was lowest in the untreated plants. Thus, while early-season floral bud removal may have reduced percentage boll retention at main stem Node 7, the slopes at this node indicated retention increased at a greater rate in the damaged plants. Finally, the quadratic component for the probability of harvesting a mature first position boll was greater in the untreated than in the most severe floral bud removal treatment (i.e., 100% removal for 3 wk), indicating that percentage fruit set was lower at the top of the canopy in the untreated control.

Table 4. Probability of harvesting a mature boll (averaged across mainstem nodes) at harvest on cotton plant sympodia in fruit removal (FR) studies conducted at Tifton, GA, in 1998 and 1999.

Treatment	N	1	2	≥3	Total
		Sympodial position			
		%			
100% FR 1 wk	230	28.3b†	16.6a	7.2c	52.1a
100% FR 2 wk	230	26.4bc	15.2ab	9.3b	51.0a
100% FR 3 wk	230	21.6d	14.2b	11.9a	47.8b
50% FR 1 wk	230	31.9a	14.4b	5.5de	51.9a
50% FR 2 wk	230	27.7b	15.8ab	6.2cd	49.6a
50% FR 3 wk	230	24.4c	14.6b	8.8b	47.8b
Untreated	230	31.9a	15.1ab	4.8e	51.7a
			ANOVA		
Source of variation					
Treatment (T)		**	NS‡	**	NS
Node (N)		**	**	**	**
T × N		**	**	**	**
df		54	54	54	54
LSD (0.05)		2.1	1.7	1.4	3.1

* Significant at $P = 0.05$.
** Significant at $P = 0.01$.
† Means followed by the same letter within a column are not significantly different ($P = 0.05$). Least square means are presented.
‡ NS = not significant.

Jenkins et al. (1990b) reported the percentage of plants with a harvestable first sympodial position boll was greatest (48.7%) at main stem Node 11 (counting the cotyledonary node as number zero) in a population density of ≈95 000 plants ha^{-1}. With a population density of ≈82 500 plants ha^{-1}, our results show the probability of harvesting a mature boll in the untreated control was greatest at main stem Node 9 (70.7%; Fig. 1). Also, as the intensity of floral bud removal increased, the main stem node of peak percentage fruit set also increased, while the maximum value of percentage fruit set decreased. For instance, with 50% floral bud removal for two consecutive weeks, maximum boll set (64.2%) occurred at main stem Node 13; and in the 100% floral bud removal for three consecutive weeks treatment, maximum boll set (51.4%) occurred at main stem Node 16 (Fig. 1). Thus, removal of early-season floral buds decreased the probability of harvesting a mature boll in the lower canopy, but increased the probability of harvesting a mature boll in the upper canopy.

Intercepts for the probability of harvesting a mature third sympodial position boll were least in the untreated and 50% floral bud removal for 1-wk treatment, and

Table 5. Regression coefficients for the probability of harvesting a mature first and third sympodial position boll in fruit removal (FR) studies conducted at Tifton, GA, in 1998 and 1999.

Effect	Treatment	Intercept		Linear		Quadratic		F
		beta	SE	beta	SE	beta	SE	
Harvestable first sympodial position bolls, %	100% FR 1 wk	30.6ab†	4.9*	6.3bc	0.43**	−0.50ab	0.029**	305**
	100% FR 2 wk	21.3bc	1.9**	7.8a	0.43**	−0.53a	0.028**	361**
	100% FR 3 wk	13.6c	3.6	6.3bc	0.40**	−0.39c	0.026**	220**
	50% FR 1 wk	34.7a	5.2*	6.9ab	0.39**	−0.55a	0.025**	460**
	50% FR 2 wk	27.7ab	3.5*	7.0ab	0.42**	−0.53a	0.028**	370**
	50% FR 3 wk	19.9bc	3.5*	6.7ab	0.39**	−0.45bc	0.025**	332**
	Untreated	38.5a	5.1*	5.4c	0.45**	−0.48ab	0.029**	263**
	LSD (0.05)	11.5		1.2		0.076		
Harvestable third sympodial position bolls, %	100% FR 1 wk	10.3bc	2.8	0.8c	0.23**	−0.10cd	0.015**	41**
	100% FR 2 wk	12.2ab	2.4*	1.7b	0.29**	−0.16b	0.019**	65**
	100% FR 3 wk	14.8a	3.8	2.6a	0.31**	−0.22a	0.021*	114**
	50% FR 1 wk	7.4c	1.8	0.7c	0.16**	−0.08d	0.010**	56**
	50% FR 2 wk	9.0bc	2.0*	0.7c	0.19**	−0.08d	0.012**	40**
	50% FR 3 wk	12.6ab	2.8*	1.2bc	0.27**	−0.13bc	0.018**	54**
	Untreated	6.7c	1.5*	0.6c	0.16*	−0.07d	0.010*	45**
	LSD (0.05)	3.8		0.7		0.044		

* Significant at $P = 0.05$.
** Significant at $P = 0.01$.
† Means followed by the same letter within a column and effect are not significantly different ($P = 0.05$). LSD is computed from the average weighted standard errors (Error means squared = $1/7 \Sigma SE^2$).

greatest in the most severely damaged plants (Table 5). These data illustrate that early-season floral bud removal resulted in increased percentage boll retention in the third sympodial position at the bottom of the plant canopy (Fig. 2). In addition, the linear component was greatest in the 100% floral bud removal for two and three consecutive weeks treatments, indicating retention increased at a greater rate in the damaged plants. Finally, the quadratic component for the probability of harvesting a mature third position boll was lesser in the untreated than in the most severe floral bud removal treatments, indicating that percentage fruit set was greater at the top of the canopy in the floral bud removal treatments.

Jenkins et al. (1990b) reported the percentage of plants with a harvestable third sympodial position boll was greatest at main stem Node 7 (counting the cotyledonary node as number zero). Our results show the probability of harvesting a mature boll was greatest in the untreated plants at main stem Node 10 (12.4%; Fig. 2). Also, as the intensity of floral bud removal increased, the main stem node of peak percentage fruit set decreased while the maximum value of percentage fruit set increased. For instance, in the 50% floral bud removal for two consecutive weeks treatment, maximum boll set (20.7%) occurred at main stem Node 9; in the 100% floral bud removal for three consecutive weeks treatment, maximum boll set (24.6%) occurred at main stem Node 8 (Fig. 2). Thus, removal of early-season floral buds increased the probability of harvesting a mature boll in the third sympodial position, particularly in the bottom of the plant canopy.

To summarize, removal of early-season floral buds in our studies increased the probability of harvesting a mature boll in more apical and distal positions. These data are in agreement with Jones et al. (1996b), who removed flowers for several weeks after anthesis. Thus, depending on main stem node and sympodial fruiting position, our results both support and refute the hypothesis outlined by Sadras (1995) that cotton might com-

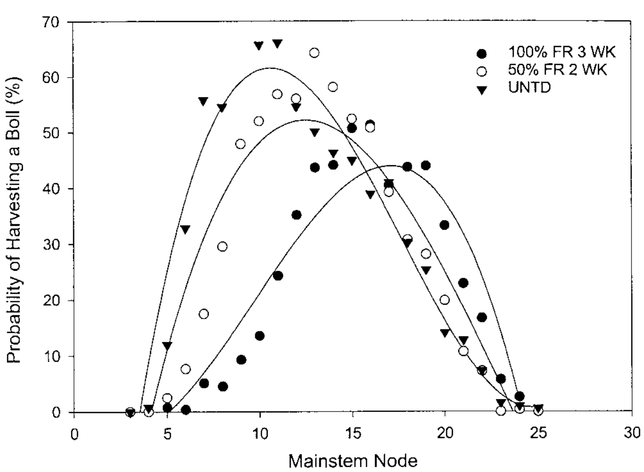

Fig. 1. Probability of harvesting a mature first sympodial position boll at each mainstem node in fruit removal studies conducted at Tifton, GA, in 1998 and 1999. Only select treatments are shown for clarity. FR, fruit removal; UNTD, untreated.

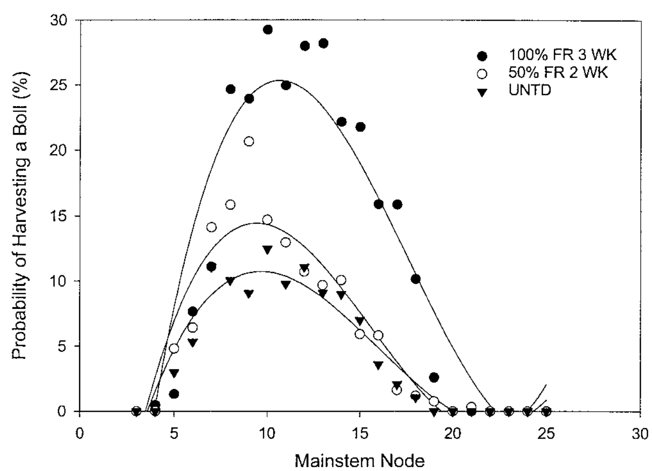

Fig. 2. Probability of harvesting a mature third sympodial position boll at each mainstem node in fruit removal studies conducted at Tifton, GA, in 1998 and 1999. Only select treatments are shown for clarity. FR, fruit removal; UNTD, untreated.

Table 6. Total seed cotton yield on cotton plant sympodia and monopodia in fruit removal (FR) studies conducted at Tifton, GA, in 1998 and 1999.

Treatment	N	Sympodial position 1	2	≥3	Monopodia	Total
		kg ha^{-1}				
100% FR 1 wk	230	2375bc†	1303ab	521c	652bc	4851ab
100% FR 2 wk	230	2309cd	1223ab	657b	916a	5105a
100% FR 3 wk	230	1907e	1233ab	927a	798ab	4865ab
50% FR 1 wk	230	2747a	1103c	375de	487c	4712b
50% FR 2 wk	230	2517b	1327a	473cd	801ab	5118a
50% FR 3 wk	230	2184d	1247ab	694b	800ab	4925ab
Untreated	230	2677a	1162bc	305e	680bc	4824ab
				ANOVA		
Source of variation						
Treatment (T)		**	*	**	*	*
Node (N)		**	**	**	NA‡	NA
T × N		**	**	**	NA	NA
df		1188	1188	1188	54	571
LSD (0.05)		151	109	100	231	314

* Significant at $P = 0.05$.
** Significant at $P = 0.01$.
† Means followed by the same letter within a column are not significantly different ($P = 0.05$). Least square means are presented.
‡ NA = not applicable.

pensate for loss of fruiting forms through increased fruit retention.

Seed cotton yields in the first sympodial position (Table 6) followed the boll set percentages discussed earlier (Table 4). Totaled across main stem nodes, first sympodial position seed cotton was greater in the untreated (2677 kg ha^{-1}) and the 50% floral bud removal for 1 wk treatment (2747 kg ha^{-1}) than all others. In the second sympodial position, only the 50% floral bud removal for two consecutive weeks treatment was different from the untreated. In the third sympodial position, however, the results were opposite those recorded in the first sympodial position. Totaled across main stem nodes, third sympodial position seed cotton was greatest in the 100% floral bud removal for 2 and 3 wk treatments (657 and 927 kg ha^{-1}, respectively) and the 50% floral bud removal for 3 wk treatment (694 kg ha^{-1}; Table 6). The third sympodial position seed cotton was least in the untreated and 50% floral bud removal for 1 wk treatment (305 and 375 kg ha^{-1}, respectively; Table 6). No treatment, however, was different from the untreated control in total seed cotton (Table 6).

Jenkins et al. (1990a) reported fruit at Sympodial Position 1 produced from 66 to 75% of the total yield. Position 2 fruit produced from 18 to 21% of the total yield. All other positions on sympodial branches produced from 2 to 4% of the total yield. Our data, collected on a population density considerably less than in Jenkins et al. (1990a), show percentage first position seed cotton decreased from 55% in the untreated to 39% in the 100% floral bud removal for 3 wk treatment. Averaged across treatments, Sympodial Position 2 fruit produced 25% of the total seed cotton yield. Sympodial Position 3 fruit produced from 6% in the untreated to 19% in the 100% floral bud removal for 3 wk treatment. Jenkins et al. (1990a) also reported that monopodial branches produced from 3 to 9% of the total yield in their studies. Depending on the level of floral bud removal, monopodial branches in our studies produced from 14 to 18% of the total yield (Table 6).

Regression coefficients for first and third sympodial seed cotton are presented in Table 7. Few differences were observed in the second sympodial position data, and are therefore not presented. For this analysis, the intercept was again set at main stem Node 7 because the slope was generally greatest at this node in the data collected.

Intercepts for first sympodial position seed cotton were greatest in the untreated and least in the most severely damaged plants (Table 7). These data illustrate early-season floral bud removal resulted in less seed cotton in the first sympodial position at the bottom of the plant canopy (Fig. 3). The linear component, however, was least in the untreated plants. Thus, while early-season floral bud removal reduced seed cotton production at main stem Node 7, the slopes at this node indicated seed cotton production increased at a greater rate in the damaged plants. Finally, the quadratic component

Table 7. Regression coefficients for first and third sympodial position seed cotton in fruit removal (FR) studies conducted at Tifton, GA, in 1998 and 1999.

Effect	Treatment	Intercept beta	Intercept SE	Linear beta	Linear SE	Quadratic beta	Quadratic SE	F
First sympodial position seedcotton, kg ha^{-1}	100% FR 1 wk	112bc	9**	25bc	1.8**	−1.96abc	0.12**	289**
	100% FR 2 wk	86cd	8**	31a	2.0**	−2.17ab	0.13**	293**
	100% FR 3 wk	56e	11*	26abc	1.8**	−1.63c	0.12**	201**
	50% FR 1 wk	128ab	15*	29ab	1.8**	−2.24a	0.12**	395**
	50% FR 2 wk	111bc	10**	29ab	1.9**	−2.21ab	0.13**	324**
	50% FR 3 wk	81de	10*	27ab	1.8**	−1.91abc	0.12**	275**
	Untreated	143a	7.6**	21c	1.9**	−1.90bc	0.13**	239**
	LSD (0.05)	28		5.2		0.35		
Third sympodial position seedcotton kg ha^{-1}	100% FR 1 wk	34ab	12	2.9cd	0.8**	−0.33bc	0.06**	38**
	100% FR 2 wk	39ab	7*	5.2b	0.9**	−0.50b	0.07**	64**
	100% FR 3 wk	52a	14	8.8a	1.2**	−0.77a	0.08**	95**
	50% FR 1 wk	23b	6	2.3cd	0.5**	−0.24c	0.04**	48**
	50% FR 2 wk	31ab	8	2.5cd	0.7**	−0.29c	0.05**	37**
	50% FR 3 wk	45ab	11	4.3bc	1.0**	−0.47b	0.07**	48**
	Untreated	20b	5*	1.8d	0.5**	−0.20c	0.04**	40**
	LSD (0.05)	27		2.22		0.17		

* Significant at $P = 0.05$.
** Significant at $P = 0.01$.
† Means followed by the same letter within a column and effect are not significantly different ($P = 0.05$). LSD is computed from the average weighted standard errors (Error Means Squared = $1/7 \sum SE^2$).

for first sympodial position seed cotton was least in the most severe floral bud removal treatment (i.e., 100% removal for 3 wk), indicating seed cotton production was greater at the top of the canopy in this treatment.

Intercepts for third sympodial position seed cotton were least, although not significantly, in the untreated and 50% floral bud removal for 1 wk treatment (Table 7). These data illustrate early-season floral bud removal resulted in greater seed cotton production at the bottom of the plant canopy (Fig. 4). In addition, the linear component was greatest in the 100% floral bud removal for two and three consecutive weeks treatments, indicating seed cotton production increased at a greater rate in these treatments. Finally, the quadratic component for third sympodial position seed cotton was lower in the untreated and 50% floral bud removal for one and two consecutive weeks treatments. These data indicate seed cotton production was greater at the top of the canopy in the treatments that were subjected to the greatest levels of floral bud removal (i.e., 100% removal for two and three consecutive weeks).

Jenkins et al. (1990a) indicated main stem Nodes 9 through 14 produced the bulk of the lint in the cultivars tested in their studies. In our studies, first sympodial position seed cotton was greatest at main stem Node 11 in the untreated, main stem Node 13 in the 50% floral bud removal for 2 wk treatment, and main stem Node 15 in the 100% floral bud removal for 3 wk treatment. Thus, the main stem node of maximum first position yield and the intensity of early-season floral bud removal were related.

CONCLUSIONS

In this study, the lowest level of early-season floral bud removal (i.e., 50% removal for 1 wk) resulted in no observable changes in spatial yield distribution. These results support the hypothesis that those floral buds damaged early in the season would have shed physiologically anyway. The probability of harvesting a mature boll was reduced in the lower plant canopy and in the first sympodial position as a result of more intense early-season floral bud removal. More intense removal of early-season floral buds, however, increased the probability of harvesting a mature boll in the upper canopy and in the third sympodial position. Thus, these results support the hypothesis that reproductive structures that may have shed physiologically (in the upper canopy and in the third sympodial position) were retained, replacing those damaged earlier in the growing season. It is possible, however, that the increased probability of harvesting a mature boll in the upper canopy and in the third sympodial position was due in part to the production of additional fruiting sites. Regardless, these modifications in spatial yield distribution adequately replaced those floral buds removed early-season, as total seed cotton yield was not different among the treatments at crop maturity.

Floral bud removal also resulted in decreased boll weight in these studies, but only in the first sympodial position. We propose that this decrease was due to the fact that the heaviest fruit produced at the bottom of the canopy was removed as floral buds and was not included for boll weight determinations at harvest. Therefore, our data lead us to reject the hypothesis indicating resources that would have been partitioned into damaged structures are partitioned into undamaged ones.

Finally, growth analyses at 90 d after planting showed that removal of early-season floral buds resulted in an increase in the number of fruiting sites. These results support the hypothesis proposing resources that would have been partitioned into damaged structures are partitioned into the production of additional fruiting sites. The production of additional fruiting sites, however, did not result in a significant delay in crop maturity.

It should be noted, however, that crop productivity in these studies was maintained at the highest possible level, resulting in an average seed cotton yield across all three studies of 4914 kg ha^{-1}. Compensatory growth after loss of floral buds has been shown to be restricted under conditions of low resource availability (i.e., low fertility, low temperature, and high plant density; Sa-

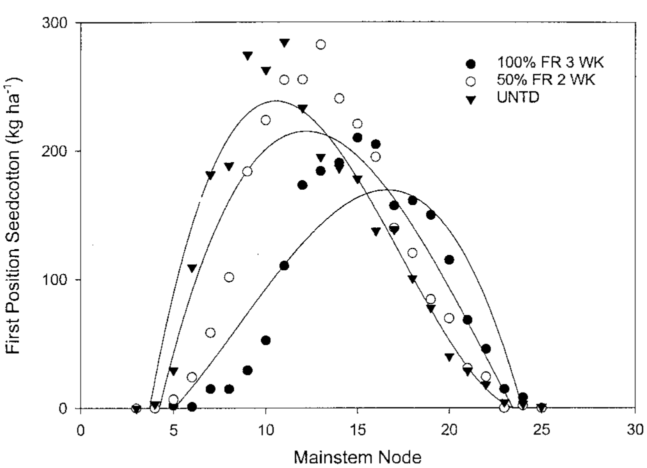

Fig. 3. First sympodial position seedcotton at each mainstem node in fruit removal studies conducted at Tifton, GA, in 1998 and 1999. Only select treatments are shown for clarity. FR, fruit removal; UNTD, untreated.

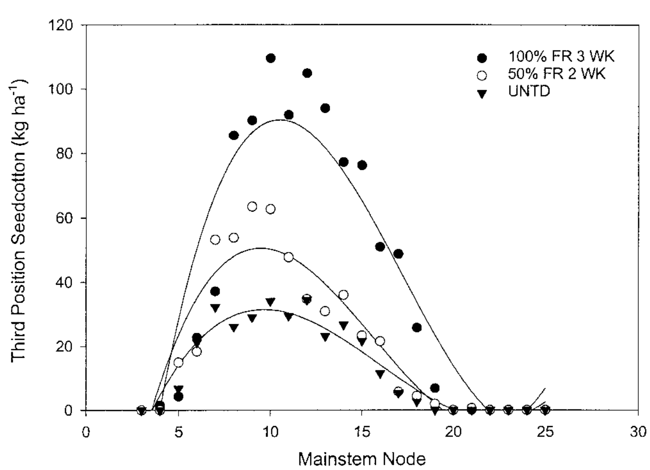

Fig. 4. Third sympodial position seedcotton at each mainstem node in fruit removal studies conducted at Tifton, GA, in 1998 and 1999. Only select treatments are shown for clarity. FR, fruit removal; UNTD, untreated.

dras, 1996). Therefore, the compensatory capacity of cotton in commercial production systems may be more variable due to local management practices and regional weather patterns.

It also should be noted that cotton in many production systems is managed to achieve the highest possible level of early-season floral bud retention (i.e., $\geq$90%). Early in the growing season (i.e., before anthesis) the majority of the floral buds present on a cotton crop are from first sympodial positions on the first seven sympodial branches. In these studies, the probability of harvesting a mature boll on any one of these positions in the untreated was never $>$70.7%. Therefore, even in the absence of plant compensatory growth as part of the economic injury level, economic thresholds should be developed to include spatial distribution of lint yield as part of the model.

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