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Comparative Growth of Obsolete and Modern Cotton Cultivars. II. Reproductive Dry Matter Partitioning[1]

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ABSTRACT

Although cotton (*Gossypium hirsutum* L.) lint yield increases have been realized as a result of plant breeding efforts, there is little documentation concerning alterations induced in reproductive growth patterns by selection processes. This study was designed to give insight into those facets of reproductive dry matter partitioning which have been altered via breeding programs based on the selection for yield. Twelve cultivars, six each from both the Stoneville and Deltapine backgrounds, were planted on either 26 Apr. or 12 May 1982. Reproductive growth was monitored at various times during the season by both numbers and dry weights of squares, immature bolls, and mature bolls. In addition, flowers were counted on a row of each plot every week during July and August. There were no significant planting date interactions regarding cultivar differences. The modern cultivars produced a greater proportion of their squares and flowers earlier than the obsolete cultivars. There were significant correlation coefficients for the relationship of cultivar release year to total flowers occurring before 90 days after planting (DAP) (r = 0.61 and 0.57 for the April and May plantings respectively). The trend of greater production of early squares and flowers results in larger amounts of early bolls in the newer cultivars. The percentage of total bolls lost due to abscission between 117 and 142 DAP is similar for most cultivars. Therefore, the greater number of bolls produced by the new cultivars at 142 DAP is attributable to the quantity present prior to shedding. The modern cultivars exhibited greater reproductive to vegetative ratios with 'STV 213', 'STV 825', 'DPL 41', and 'DPL 16' having 0.95, 0.86, 0.84, and 0.71 kg reproductive dry weight/kg vegetative dry weight at 117 DAP, respectively. The modern cultivars appear to produce a larger lint yield by two major processes. The first is a greater partitioning of dry matter to reproductive organs. The second is an increased amount of reproductive development occurring when maximal leaf mass and area are present.

Additional index words: ***Gossypium hirsutum*** **L., Reproductive to vegetative ratio, Square production, Boll production, Cotton fruiting.**

HEARN (9) suggested that cultivar differences in cotton (*Gossypium hirsutum* L.) yield are primarily due to differences in reproductive sinks, rather than photosynthetic capacity. Essentially, selection for yield has resulted in genotypes with reproductive growth that occurs earlier in relation to the age of the vegetative organs, and therefore exhibits a greater synchrony with assimilatory activity. Manifestation of such a relationship has often been observed with high yielding cultivars having fewer nodes and larger bolls (10). Bhardwaj et al. (3) found that dwarf, small leaf area genotypes tended to yield more seed cotton and exhibited greater fruiting coefficients (ratio of seedcotton to total dry matter produced). Similarly, Karami and Weaver found a greater yield in an okra-leaf isoline compared to its normal counterpart, which was a taller plant with a smaller harvest index (12).

A wide variety of phenomena are involved in the initiation and development of reproductive growth. For example, Hearn (11) suggested that reproductive sink development depends on the occurrence of the first flower, the time interval between successive flowers, and the rate of boll growth. In addition, it has long been recognized that early flower production results in a greater proportion of open bolls early in the season compared to those resulting from flowers produced later in the season (6). Verhalen et al. (15) found a linear decrease in the percentage of bolls set as the season progresses in six cultivars which exhibited significant differences. Similarly, Ewing (8) recognized the importance of rapid flower production combined with a low rate of boll shedding in lint production. Wanjura and Newton (16) suggested that cultivars require similar periods of time to complete boll setting and any differences in maturity are due to variations in occurrence of the first flower and the rate of boll setting during the reproductive cycle.

Although selection for lint production has been shown to result in numerous alterations in the components of yield (4, 14), little is understood concerning these genetically induced changes in reproductive dry matter partitioning throughout the season. This study was initiated to determine the variations in reproductive growth and their attendant associations with vegetative growth, which have occurred as a result of the progressive development of cotton cultivars exhibiting an incremental array of potential yields.

MATERIALS AND METHODS

Twelve cotton cultivars, six each from the Stoneville (STV) and Deltapine (DPL) backgrounds and representing lines which have been released since 1900, were grown during 1982 at Stoneville, MS. The cultivars were planted in 5 row plots with rows 1 m wide and 7.5 m long on either 26 April or 12 May. Throughout the season an intensive insecticide spray regime was implemented to assure that insect damage did not confound the observations. All other cultural practices and aspects of experimental design are described in a previous manuscript (17).

One completely bordered row was used for destructive sampling. Growth was determined at 38, 52, 69, 96, 117, and 142 days after planting (DAP) for the 26 April planting, and at 36, 53, 80, 101, 126, and 139 DAP for the 12 May planting. Harvests at the first 3 dates utilized 0.6 m of row while harvests thereafter used 0.3 m of row. Plants of each section of row were separated into vegetative organs, squares, mature (boll walls open 1 cm) bolls, and immature (closed) bolls at various measurement dates. Their numbers were recorded and the different parts were dried at 70°C prior to dry weight determination. Vegetative dry weight partitioning will be presented in an accompanying paper (17). Following initiation of flowering, bloom counts of white flowers were made in the completely bordered, nondestructive sampling row once every week to estimate flower production. Flower counts were continued until flowering ceased late in August. From the dry weight of reproductive and vegetative plant portions (17) a repro-

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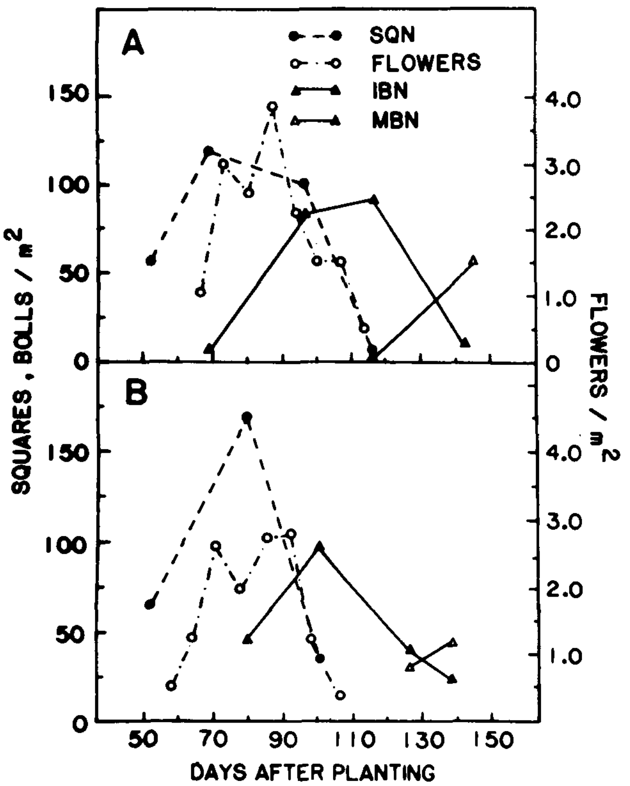

Fig. 1. Overall mean number of squares, white flowers, immature bolls, and mature bolls at various dates after the A) 26 Apr. 1982 and B) 12 May 1982 planting dates.

ductive to vegetative ratio (RVR) was calculated for each cultivar and harvest.

RESULTS

The number of squares, bolls, and flowers averaged across cultivar for both planting dates are shown in Fig. 1. Generally, the trends in reproductive organ development were similar for each planting date. Both exhibited comparable patterns of squares, flowers, immature bolls, and mature bolls at similar periods of growth. Analysis of the effect of planting date on reproductive parameters at similar chronological points in growth did not reveal significant planting date interactions. In addition, analysis of variance components indicated no significant effect of cultivar background (Stoneville or Deltapine). The data presented will be mainly measurements from the April planting, since they are representative of the cultivar relationships found at both plantings.

Eight cultivars had a maximal number of squares (SQN) at 69 DAP, while 'STV 5A', 'Lone Star', 'DPL 11', and 'Lightning Express' produced their peak square number at 96 DAP (Table 1). The squares formed at 69 DAP numbered 151, 150, 144, and 137 per m² for 'STV 825', 'DPL 16', 'STV 213', and 'DPL 41', respectively. In addition to the differences in the occurrence of maximal SQN, the total number of squares measured over all dates were variable, with Lightning Express and Lone Star possessing the largest and smallest numbers, respectively. Generally, the square dry weight (SQDW) (Data not shown) reflected the same cultivar differences shown by SQN.

Table 1. Square number, measured at various dates, of 12 cotton cultivars planted on 26 Apr. 1982.

Cultivar	Year of release	Days after planting 38	52	69	96	117
		squares/m²				
STV 825	1978	4.1	73.8	150.6	86.4	0.5
STV 213	1962	5.5	73.0	143.8	60.1	0.5
STV 2B	1938	0.5	51.4	116.2	90.2	0.0
STV 5A	1938	2.2	59.0	121.6	132.3	3.8
STV 2	1933	2.5	59.0	128.5	82.5	1.1
Lone Star	1905	3.0	40.2	49.5	133.4	19.7
DPL 41	1976	5.2	53.6	137.5	80.4	3.8
DPL 16	1965	3.6	54.9	150.3	101.7	8.7
DPL 14	1941	3.8	50.8	96.5	90.2	12.0
DPL 11	1932	0.8	58.2	110.7	129.6	3.8
Dixie Triumph	1914	1.6	49.5	124.1	80.4	6.6
Lightning Express	1905	3.6	62.9	133.7	160.2	1.1
$LSD_{0.05}$		NS	17.5	30.2	48.1	8.8

Table 2. Number of white flowers produced on various dates by 12 cotton cultivars planted on 26 Apr. 1982.

Cultivar	Year of release	Days after planting 65	78	80	87	94	101	107	114
		flowers/m²							
STV 825	1978	1.4	3.3	3.9	4.9	2.8	1.6	1.2	0.5
STV 213	1962	1.4	3.3	3.0	4.1	2.5	0.9	0.7	0.3
STV 2B	1938	0.8	3.1	2.1	2.4	1.7	1.5	1.3	0.5
STV 5A	1938	0.9	2.4	2.6	4.7	2.4	1.8	2.6	0.9
STV 2	1933	1.1	3.2	2.4	3.5	2.0	1.3	1.2	0.3
Lone Star	1905	0.5	1.2	0.7	1.4	1.2	1.7	2.6	1.2
DPL 41	1976	1.5	4.4	3.8	5.6	2.5	1.2	1.0	0.5
DPL 16	1965	1.0	3.7	2.3	4.3	2.0	1.7	1.3	0.8
DPL 14	1941	0.8	3.5	2.8	3.3	1.9	1.4	1.9	0.8
DPL 11	1932	0.5	3.0	2.4	4.4	2.3	1.9	2.1	0.8
Dixie Triumph	1914	0.9	2.8	2.0	3.6	2.7	1.8	1.2	0.5
Lightning Express	1905	1.9	2.5	2.6	4.9	3.6	2.5	2.1	0.5
$LSD_{0.05}$		0.4	1.0	0.8	1.2	0.7	0.7	0.7	0.4

By 65 DAP all cultivars displayed measurable flowering activity (Table 2). Following this date there was an increase in the number of white flowers counted for all cultivars with a maximum at 87 DAP for 9 of the 12 entries. 'STV 2B', Lone Star, and 'DPL 14' exhibited maxima at 74, 107, and 74 DAP, respectively. STV 825, STV 213, and DPL 41 produced 69.2, 72.8, and 74.6% of the total counted white blooms prior to 90 DAP. Lone Star, 'Dixie Triumph', and Lightning Express produced 60% or less of their total number of white flowers by this time. Correlations for the relationship between cultivar release year (RYR) and the number of flowers counted on the various dates support this observation (Table 3). Through 87 DAP for the April planting date, and 91 DAP for the May planting, there were significant positive correlations for the relationship. After these dates, there were either no correlations or significant negative correlations.

When the cultivars are grouped according to their RYR, the trend in flowering is easily observed (Fig. 2). The new cultivars (1950-present) displayed a greater increase in blooms between 70 and 90 DAP than either the intermediate (1920-1950) or the old (1900-1920) cultivars. Between 90 and 10 DAP a transitional period occurred, after which, the old and intermediate cultivars exhibited greater flower numbers than found in the new cultivars.

Table 3. Simple correlation coefficients for the relationship between cultivar release year and the number of white flowers counted on varying dates for both planting dates.

Days after planting	Planting date: 26 Apr.	12 May
	r	
58	--	0.34**
64	--	0.39**
65	0.24*	--
71	--	0.62**
74	0.51**	--
78	--	0.39**
80	0.61**	--
85	--	0.58**
87	0.40**	--
91	--	0.23*
94	0.04	--
98	--	0.11
101	−0.34**	--
107	−0.42**	−0.25*
114	−0.15	--

*,** Significant at the 0.05 and 0.01 level, respectively.

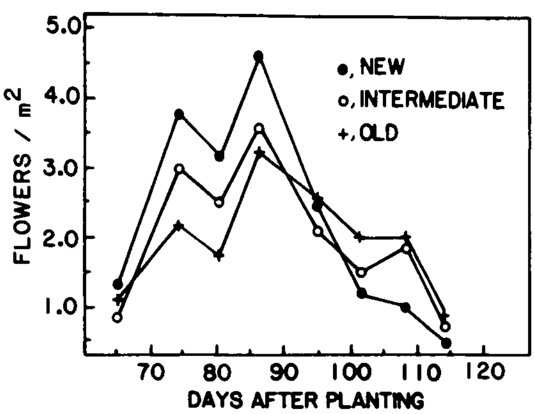

Fig. 2. Mean number of white flowers occurring at different dates for the cultivars grouped by their year of release and planted on 26 Apr. 1982 (new = 1950 to present; intermediate = 1920 to 1950; old = 1900 to 1920).

By 69 DAP, the immature boll numbers (IBN) ranged from 4.9/m^2 for Lone Star to 22/m^2 for 'STV 2' (Table 4). The development from that date until 96 DAP was significant and exhibited a large cultivar effect. The IBN ranged from 25 for Lone Star to 120/m^2 for STV 825 at 96 DAP. Of the cultivars released before 1950 only Lightning Express displayed IBN greater than any cultivar released after 1950. There were significant correlations for the relationships between RYR and both IBN and immature boll dry weight (IBDW) (Table 5). At 69 and 96 DAP significant correlation coefficients of 0.22 and 0.48, respectively, were found for the relationship of RYR to IBN for the April planting. The relationship between RYR and IBDW was significant at 96 and 117 DAP (r = 0.48 and 0.37). At 142 DAP the relationship between RYR and IBDW was significant and negative. The relationships found in the May planting were similar to those of the April date except there were no significant correlations between RYR and either IBN or IBDW at 139 DAP.

Following 96 DAP, some cultivars (STV 825, STV 2B, DPL 16, and DPL 14) declined in IBN while IBDW continued to increase for all cultivars (Table 4). The reduction in IBN was largely due to boll opening, since the number of mature bolls (MBN) at 117 DAP accounted for most of the decrease in all cultivars except STV 2B. At 117 DAP and later, positive correlations for the association between RYR and both MBN and mature boll dry weight (MBDW) were evident regardless of the date of planting (Table 5).

Table 4. Number and dry weight of immature and mature bolls, measured at various dates, of 12 cotton cultivars planted on 26 Apr. 1982.

Cultivar	Year of release	Immature 69	Immature 96	Immature 117	Immature 142	Mature 117	Mature 142
		Bolls/m^2					
STV 825	1978	7.9	120.3	107.1	18.0	12.0	70.0
STV 213	1962	10.4	97.9	119.2	6.6	6.0	80.4
STV 2B	1938	6.3	94.6	76.5	12.6	2.7	45.4
STV 5A	1938	7.7	81.5	89.1	27.3	4.4	41.0
STV 2	1933	11.0	62.9	67.2	12.6	1.1	33.3
Lone Star	1905	2.5	24.6	66.1	28.4	0	20.8
DPL 41	1976	10.4	96.2	101.1	4.9	7.7	71.6
DPL 16	1965	8.5	115.3	110.4	20.2	2.7	74.3
DLP 14	1941	3.8	94.6	88.0	8.2	6.6	66.7
DLP 11	1932	5.2	80.4	92.4	10.4	2.7	50.3
Dixie Triumph	1914	4.4	76.5	94.0	7.7	1.6	55.8
Lightning Express	1905	9.0	105.0	125.2	13.1	7.6	77.6
$LSD_{0.05}$		NS	28.6	27.7	14.7	6.2	18.9
		Boll dry weight (g/m^2)					
STV 825	1978	2.0	247.0	532.3	70.2	65.1	409.4
STV 213	1962	2.3	231.1	581.8	30.9	27.8	448.5
STV 2B	1938	3.1	211.1	380.0	70.7	16.5	314.3
STV 5A	1938	2.5	138.8	331.4	77.6	25.6	296.4
STV 2	1933	3.3	132.2	352.5	69.3	6.8	225.2
Lone Star	1905	0.8	57.4	194.8	187.5	0	142.3
DPL 41	1976	3.1	189.9	435.7	21.5	35.3	449.3
DPL 16	1965	3.6	281.3	506.8	80.7	19.1	489.3
DPL 14	1941	1.7	230.2	393.7	38.3	30.1	413.4
DPL 11	1932	1.6	147.4	275.7	78.3	14.4	264.4
Dixie Triumph	1914	2.9	162.5	444.2	40.0	9.9	326.9
Lightning Express	1905	2.7	178.8	461.9	47.8	49.6	390.1
$LSD_{0.05}$		NS	76.4	148.7	68.9	34.9	115.6

Figure 3 shows the total number of bolls of the cultivars grouped by RYR. The old cultivars displayed a much slower increase in boll number between 69 and 96 DAP than both the intermediate and new cultivars. After 96 DAP, the old cultivars continued producing bolls in a similar fashion whereas the new and intermediate cultivars increased at a much slower pace. At 117 DAP the new, old, and intermediate cultivars had 114, 99, and 85 total bolls, respectively. These differences are confirmed by the positive correlation coefficients for the relationship between RYR and both total boll dry weight and total boll number late in the season for both planting dates (Table 5).

The newer cultivars partitioned a greater proportion of their dry matter into reproductive plant portions after 69 DAP for the April planting (Table 6). Throughout the season the reproductive to vegetative ratio (RVR) increased reflecting both the growth of reproductive organs and late season loss of leaves and petioles. At 117 DAP, the four newest cultivars exhibited values of 0.71 kg/kg or larger, the highest

Table 5. Simple correlation coefficients of the relationships between year of cultivar release and various parameters of reproductive growth at numerous harvests of each planting date.

Variable	52	53	69	80	96	101	117	127	139	142
	Days after planting									
	r									
	26 Apr.†									
Square number (SQN)	0.28**	--	0.43**	--	−0.36**	--	−0.22**	--	--	--
Immature boll number (IBN)	--	--	0.22*	--	0.48**	--	0.21	--	--	−0.12
Mature boll number (MBN)	--	--	--	--	--	--	0.30*	--	--	0.40**
Total boll number (TBN)	--	--	0.22*	--	0.48**	--	0.26*	--	--	0.34**
Square dry weight (SQDW)	0.15	--	0.37**	--	0.27**	--	0.00	--	--	--
Immature boll dry weight (IBDW)	--	--	0.10	--	0.48**	--	0.37**	--	--	−0.25*
Mature boll dry weight (MBDW)	--	--	--	--	--	--	0.24*	--	--	0.48**
Total boll dry weight (TBDW)	--	--	0.10	--	0.48**	--	0.40**	--	--	0.37**
RVR‡	0.17	--	0.39**	--	0.50**	--	0.61**	--	--	0.53**
	12 May									
Square number (SQN)	--	0.20	--	0.01	--	−0.21	--	--	--	--
Immature boll number (IBN)	--	−0.04	--	0.37**	--	0.37**	--	−0.02	0.05	--
Mature boll number (MBN)	--	--	--	--	--	--	--	0.41**	0.60**	--
Total boll number (TBN)	--	--	--	0.37**	--	0.37**	--	0.28*	0.54**	--
Square dry weight (SQDW)	--	0.05	--	0.07	--	−0.25*	--	--	--	--
Immature boll dry weight (IBDW)	--	−0.02	--	0.40**	--	0.42**	--	−0.09	−0.01	--
Mature boll dry weight (MBDW)	--	--	--	--	--	--	--	0.43**	0.56**	--
Total boll dry weight (TBDW)	--	--	--	0.40**	--	0.42**	--	0.30*	0.48**	--
RVR	--	0.08	--	0.45**	--	0.47**	--	0.54**	0.72**	--

*,** Significant at the 0.05 and 0.01 levels, respectively.
† Planting date.
‡ Reproductive to vegetative ratio.

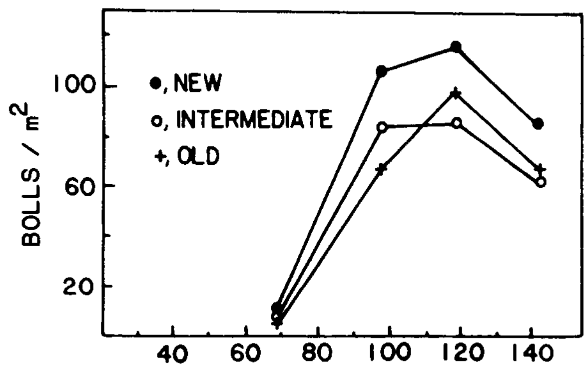

Fig. 3. Mean number of total bolls occurring at different dates for the cultivars grouped by their year of release and planted on 26 Apr. 1982 (new = 1950 to present; intermediate = 1920 to 1950; old = 1900 to 1920).

Table 6. Reproductive ratio, determined at various dates, for 12 cotton cultivars planted on 26 Apr. 1982.

Cultivar	Year of release	69	96	117	142
		Days after planting			
		kg reprod. dry wt/kg veg. dry wt			
STV 825	1978	0.06	0.37	0.86	0.92
STV 213	1962	0.07	0.37	0.95	0.96
STV 2B	1938	0.06	0.28	0.62	0.74
STV 5A	1938	0.06	0.19	0.44	0.65
STV 2	1933	0.06	0.18	0.57	0.65
Lone Star	1905	0.03	0.09	0.20	0.40
DPL 41	1976	0.08	0.34	0.84	1.12
DPL 16	1965	0.07	0.34	0.71	0.95
DPL 14	1941	0.05	0.34	0.60	0.94
DPL 11	1932	0.05	0.21	0.41	0.90
Dixie Triumph	1914	0.07	0.28	0.61	0.85
Lightning Express	1905	0.06	0.21	0.60	0.86
$LSD_{0.05}$		0.01	0.12	0.19	0.19

values found at that date. The correlations of cultivar release year to RVR are 0.39 or larger after 69 DAP for the April planting date and 0.45 or larger after 80 DAP for the May planting date (Table 5).

DISCUSSION

The data support the supposition that recently released cultivars partition a greater proportion of growth into reproductive than vegetative plant parts. This observation was supported by the number of bolls, the dry weight of the bolls, and the RVR of the cultivars. Bhardwaj et al. (3) described an inefficient genotype as one which was tall, possessing a large number of sympodial branches, and a large leaf area index (LAI). Such inefficient lines also exhibited smaller fruiting coefficients and yield of seed cotton. Both the vegetative parameters reported earlier (17) and the reproductive parameters presented in this report agree with these conclusions. The modern cultivars accumulated less mass in their vegetative portions and greater mass in their reproductive portions.

In addition to the quantity of reproductive matter produced, the timing of the reproductive growth with respect to the vegetative growth, appears to have undergone a considerable alteration in response to breeding efforts. The modern cultivars (released since 1950) produced at least 70% of their total counted squares before 70 DAP, a greater proportion than any of the other lines. Since all cultivars had produced squares by 38 DAP, the greater square production of the modern cultivars does not appear to be due to an earlier square initiation. The production of flowering sites is closely tied to vegetative growth since it is responsible for production of both new sympodia and additional nodes on existing sympodia (13). In light of the vigorous vegetative growth of the obsolete cultivars, it is likely that the older cultivars lost a greater number of squares as a result of shedding. One important cause of square shedding is insect damage during reproductive growth (9). Since there was no attempt to quantify this effect, there is a possiblity that differences in insect sensitivity existed among the cultivars. However, throughout the course of this study an intensive effort was made to reduce the amount of insect damage via regular insecticide applications. In light of both the insecticide treatments and visual observations, we do not believe that insect damage played a major role in producing the cultivar differences observed.

Regardless of the means by which the square numbers were altered, there was a positive correlation for the relationship between the proportion of squares counted before 70 DAP and the proportion of flowers counted before 90 DAP ($r = 0.72$). In addition, all cultivars reached a critical LAI (5) by 78 DAP and a maximal LAI at 96 DAP with declining values thereafter (17). These data suggest that more intensive early square and flower production of the modern cultivars resulted in a greater number of developing bolls occurring concurrently with maximal LAI and light interception. The loss of leaf weight and LAI after 96 DAP is indicative of net leaf loss due to the plant's inability to replace senescing leaves. This response is due in part to the dominant reproductive sink activity occurring at that time. These observations support the suggestion of Hearn (11) that differences in cultivar lint production are largely due to the relative amount of reproductive growth which occurs when peak LAI and leaf mass is available.

Canopy photosynthesis measurements have indicated that cotton LAI values of approximately 3 to 4 result in maximal assimilatory activity (2). This indicates that a greater LAI would not increase canopy photosynthetic capacity and may induce increased shedding of bolls at lower portions of the plant canopy due to increased shading (9). There are indications of the importance of sufficient LAI during early boll development. Ashley et al. (1) found a positive correlation between the number of bolls and the LAI during early reproductive growth. During later portions of the season a negative relationship was observed.

According to Hearn (10, 11), when the growth rate of bolls is equal to the crop growth rate (CGR), the transition from vegetative to reproductive growth is complete. This phenomenon is indicative of sufficient reproductive sink activity to utilize all available photosynthate. Only Lone Star and Dixie Triumph displayed an increase in total dry weight in a previous report (17) which was greater than the growth rate of the bolls for the period from 96 to 117 DAP. Thus, only these two cultivars still possessed positive vegetative growth rates during this period. However, seven other cultivars (STV 825, STV 213, STV 5A, DPL 41, DPL 14, DPL 11, and Lightning Express) had continued stem dry weight increases from 96 to 117 DAP (17). In these cases, there were net losses of vegetative dry weight because leaf dry weight losses were greater than stem dry weight increases. Hearn's (10) theory that all assimilates were routed to the bolls once the boll growth rate equalled the CGR is incorrect in these instances, since partitioning of dry matter to the stems was still occurring in these cultivars.

Ehlig and Le Mart (7) found that boll retention was primarily a function of the number of bolls present on a plant. In this study, a net loss of bolls was not observed until the final measurement period, when all cultivars displayed considerable boll abscission (total bolls at 117 DAP − total bolls at 142 DAP). This response indicates that all cultivars had a greater number of bolls at 117 DAP than what could be sustained by the plant. The losses during the period in question ranged from a high of 36% for DPL 11 to a low of 17% for DPL 16. Most cultivars lost approximately 30% of their bolls during this period. The modern cultivars did not have a lower proportion of boll abscission, but they did have more bolls per unit area at the earlier reproductive periods. The result is a greater number of bolls at the final measurement. Again, this suggests that the early boll development period is of utmost importance in determination of the final yield.

In retrospect, the results suggest that two mechanisms of major importance have undergone alteration as a consequence of selection processes aimed towards greater lint yield. The first is an increased amount of dry matter routed into reproductive growth. The second is the production of a greater proportion of reproductive constituents earlier in plant development with a greater amount of the fruit development occurring during the presence of greater LAI. Additionally, the role that reproductive initiation plays in the cessation of vegetative growth, and hence to a degree of determinacy, appears important although difficult to assess.

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