

Heterosis in Upland Cotton. I. Growth and Leaf Area Partitioning¹

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ABSTRACT

There is relatively little information concerning the physiological alterations that are related to heterosis in cotton *Gossypium hirsutum* L.). To better understand this phenomenon, growth and partitioning of dry matter in four established upland cotton cultivars and their F₁ hybrid progeny were monitored in three environments. Total biomass was greater in hybrids than their parents in all environments. Growth analysis found that heterosis greatly affected early development of the hybrids. Although increases in leaf area were greater in the progeny, they were proportional to the dry weight growth of the plant, resulting in similar leaf area partitioning (LAP) coefficients for both parents and hybrids. The greater leaf area index of the hybrids, resulting from greater net assimilation rates but similar LAP values, further stimulates growth via greater interception of light and associated photosynthate production prior to the advent of significant interplant competition.

Additional index words: *Gossypium hirsutum* L., Growth analysis, Hybrid, Lint yield, Vegetative biomass.

THE INCREASED economic productivity of cotton (*Gossypium hirsutum* L.) associated with heterosis of interspecific (5, 8) and intraspecific (7, 12, 13) hybrids is a well-studied phenomenon. Despite these numerous research efforts, only a few studies have addressed either the physiological processes related to the expression of heterosis or those facets of growth associated with greater lint production (1, 9).

White and Richmond (20) attributed lint yield heterosis to greater vegetative dry matter production. Muramoto et al. (14) suggested that greater leaf area expansion rates could be involved in the expression of heterotic growth. They found this to be true for an interspecific hybrid and, to a lesser extent, for an intraspecific hybrid. More recently, Potter and Jones (15) demonstrated that leaf area partitioning is an important determinant of growth in response to varying temperatures and across a number of species representing a number of families. Herein, we report on the augmented growth responses present in intraspecific upland cotton hybrids with particular attention given to the partitioning of dry matter into leaf area.

MATERIALS AND METHODS

Four established upland cotton cultivars, 'Stoneville 825', 'Coker 3114', 'Deltapine 90', and 'MD 82ne' and their six possible hybrid combinations were grown in three field environments during 1983 at Stoneville, MS. Although reciprocal crosses were made, the resulting seed was bulked and no attempt was made to identify maternal and paternal effects. In each environment all 10 entries were grown in a randomized, complete block design with five replications.

Environments (ENV) 1 and 2 were planted at the same location on 27 April and 27 May, respectively. Environment 3 was planted on 27 April but at a different location, approximately 1.5 km away. Environments 1 and 2 consisted of a Dundee silty clay (fine-silty, mixed, thermic Aeric Ochraqualf) while ENV 3 was a Dubbs silt loam (fine-silty, mixed, thermic Typic Hapludalf). The plants were grown in plots of five, 7.5 m long rows at a width of 1 m. There were 10 plants m⁻¹ of row.

Parameters of growth were determined at five different times for each environment. The measurements were made at similar growth stages classified by dry weights and reproductive development. The stages were defined as (i) seedling, (ii) vegetative, (iii) floral bud development, (iv) early boll development, and (v) later boll development (no boll opening yet observed). Plants from 0.3 m of row were separated into stems (petioles + branches), leaves, floral buds, and bolls. The number of floral buds and bolls was recorded. Twenty leaves taken as a representative subsample of the various leaf ages and positions on one plant were removed for leaf area determination with a LI-COR Model LI-3000³ area meter. The leaf area and dry weight of this sample were used to calculate the specific leaf weight (SLW) of the leaves. The leaf area index (LAI) = (total leaf dry weight/SLW) was expressed as m² leaves/m² ground. All dry weights were determined following drying for 72 h at 70°C.

Relative growth rates of both dry weight (RGR) and leaf area (RLAGR), crop growth rate (CGR), and net assimilation rate (NAR) were calculated according to Radford (16). The method used to calculate NAR assumed that LAI and dry weight were linearly related. Leaf area partitioning coefficients (LAP) were calculated by the methods of Potter and Jones (15). Since growth parameters were not measured at emergence, it was assumed that all entries were equal and had a seedling dry weight of 0.5 g, LAI = 5×10^{-3} , and took 8 days to germinate.

Seedcotton was harvested from one row, at three harvests for all environment. Total lint yield and yield components were determined by earlier described methods (18).

The data were analyzed via analysis of variance with environment as the whole unit, and with genotype as subunit. The relationships between RGR and various parameters of growth (RLAGR, NAR, and LAP) and the increase in total dry weight and LAI over time were analyzed by subunit regression, wherein nonsignificant model parameters were pooled with the appropriate error and analyses were continued until only significant model parameters remained. The plotted RGR values represent the predicted values plus the residual. The distance the plotted points lie from the predicted regression line represent the variation not explained by the regression equation.

RESULTS AND DISCUSSION

The quantity of lint produced by the hybrids was 14% greater than that produced by the parental lines (Table 1). This trend was consistent among environments. The increased lint production was most closely associated with the weight per boll rather than with the number of bolls produced. Additionally, the percentage of the crop harvested at the first harvest was generally greater in the hybrids, indicating an earlier

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Table 1. Lint productivity and yield components of the parents and their hybrid progeny. Values represent means taken across three harvests and three growth environments.

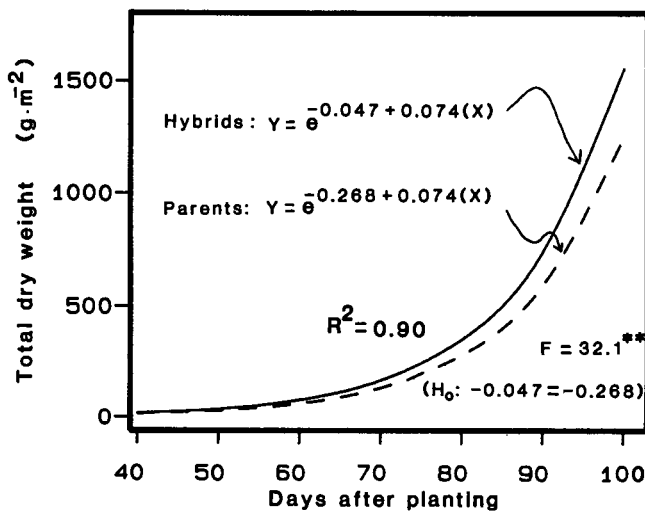
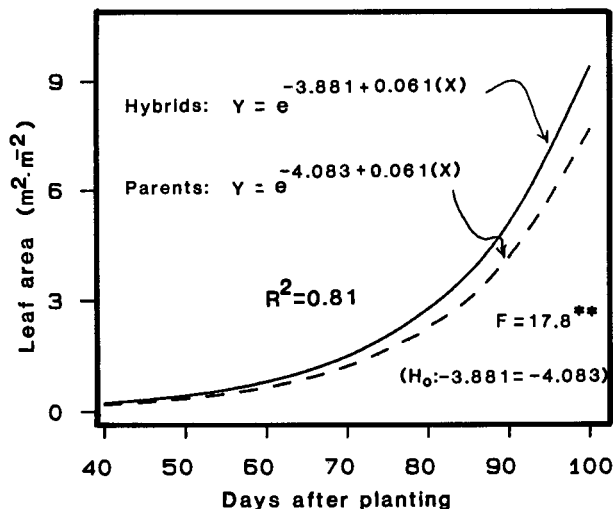
Genotype	Cumulative lint†	Cumulative bolls†	Weight per boll	Lint percentage	First harvest percentage‡	Seed index	Lint index	Seed per boll
	kg ha ⁻¹	no. m ⁻²	g	%	%	g seed ⁻¹ × 100	g lint seed ⁻¹ × 100	no.
MD 82ne (M)	1435	74	4.94	38.1	58.2	11.8	7.3	26
Stoneville 825 (S)	1480	88	4.38	36.8	54.7	10.6	6.2	26
Coker 3114 (C)	1454	77	4.60	39.4	58.6	9.9	6.5	28
Deltapine 90 (D)	1443	84	4.49	37.8	52.3	10.0	6.1	28
Parent mean	1453**	81	4.60**	38.0	55.9**	10.6	6.5	27*
C × S	1617	82	4.86	38.1	64.0	10.5	6.5	29
C × M	1764	84	5.06	39.2	65.6	10.8	6.9	29
C × D	1656	83	5.01	37.9	63.5	10.5	6.4	30
M × S	1623	81	4.96	38.2	60.3	11.3	7.0	27
D × M	1648	82	5.11	38.2	57.1	10.9	6.7	29
D × S	1616	88	4.79	37.5	53.3	10.5	6.3	29
Hybrid mean	1654**	83	4.97**	38.2	60.6**	10.8	6.6	29*
LSD (0.05)§	144	8	0.15	0.4	6.5	0.3	0.2	1

*,** Hybrid and parent means were significantly different at the 0.05 and 0.01 levels of probability, respectively.

† Cumulative of all harvests.

‡ Percentage of the total lint yield, which was harvested on the first harvest date.

§ LSD (0.05) for the difference between individual genotypes.

**Fig. 1. Subunit regression of total dry weight of the hybrids and their parents over time. The *F* values are for the comparison of the curves resulting from the hybrids and parents.****Fig. 2. Subunit regression of leaf area indices of the hybrids and their parents over time. The *F* values are for the comparison of the curves resulting from the hybrids and parents.****Table 2. Crop growth rate of the parents and their hybrid progeny. Values represent means taken across environments.**

Genotype	Harvest interval†				
	1	2	3	4	5
	g m ⁻² ground day ⁻¹				
MD 82nd (M)	0.3	1.9	5.4	13.1	16.4
Stoneville 825 (S)	0.3	1.7	5.1	12.3	15.8
Coker 3114 (C)	0.3	1.6	5.3	14.7	15.2
Deltapine 90 (D)	0.3	1.5	5.0	13.3	16.7
Parent mean	0.3**	1.7**	5.2**	13.4**	16.0**
C × S	0.5	2.8	6.9	16.8	21.5
C × M	0.4	2.3	7.6	16.0	20.7
C × D	0.4	2.4	5.9	16.5	24.8
M × S	0.4	2.1	5.9	15.4	22.6
D × M	0.3	2.1	6.1	17.8	22.1
D × S	0.3	2.2	6.4	15.6	24.9
Hybrid mean	0.4**	2.3**	6.5**	16.4**	22.8**
LSD (0.05)‡	0.1	0.6	1.6	3.3	6.4

** Hybrid and parents means were significantly different at the 0.01 level of probability.

† Harvest intervals are: 1 = seedling, 2 = vegetative growth, 3 = floral bud development, 4 = early boll development, and 5 = late boll development.

‡ LSD for the difference between the individual genotypes during the same harvest interval.

maturity. Yield components associated with dry matter partitioning within a boll (lint percentage, lint index, seed index, and seed per boll) did not differ nearly as much, indicating the additive effect of these components on the weight per boll. These increases in lint production were similar to those reported earlier for other hybrid-parent comparisons (11).

Regression analysis of the increase in both total dry matter and LAI over time resulted in exponential curves significantly different for the hybrids and the parents (Fig. 1 and 2). This difference was attributable to differing *y*-intercepts, indicating that very early growth patterns were the basis upon which later growth differences were founded. Actual means calculated across environments showed that the progeny produced 32% greater total dry matter and 29% greater leaf area than the parents prior to the last dry matter harvest. Marani and Avieli (9) did not find significant differences between a *G. hirsutum* intraspecific hybrid

Table 3. Relative growth rates (RGR), relative leaf area growth rate (RLAGR), net assimilation rate (NAR), and leaf area partitioning coefficients (LAP) of the parents and their hybrid progeny during the first two harvest intervals.

Genotype	RGR		RLAGR		NAR		LAP	
	Harvest intervals†							
	1	2	1	2	1	2	1	2
	g g ⁻¹ day ⁻¹		m ² m ⁻² day ⁻¹		g m ⁻² day ⁻¹		m ² day ⁻¹ per g day ⁻¹	
MD 82ne (M)	0.104	0.120	0.109	0.138	9.4	10.0	0.012	0.016
Stoneville 825 (S)	0.104	0.117	0.108	0.137	9.5	9.8	0.012	0.015
Coker 3114 (C)	0.103	0.116	0.107	0.131	9.4	9.4	0.011	0.015
Deltapine 90 (D)	0.098	0.110	0.106	0.124	8.3	8.9	0.013	0.016
Parent mean	0.102**	0.116*	0.108**	0.133	9.2**	9.5*	0.012	0.016
C × S	0.114	0.134	0.118	0.153	10.5	11.4	0.011	0.015
C × M	0.110	0.124	0.116	0.135	9.7	10.3	0.012	0.014
C × D	0.106	0.138	0.112	0.149	9.5	11.6	0.012	0.014
M × S	0.107	0.123	0.112	0.138	9.6	10.1	0.012	0.016
D × M	0.104	0.130	0.110	0.142	9.2	10.5	0.012	0.015
D × S	0.104	0.135	0.119	0.155	9.5	11.0	0.012	0.016
Hybrid mean	0.108**	0.131*	0.115**	0.145	9.7**	10.8*	0.012	0.015
LSD (0.05)‡	0.006	NS§	0.006	NS	0.6	NS	NS	NS

*,** Hybrid and parent means were significantly different at the 0.05 and 0.01 levels of probability, respectively.

† Harvest intervals are: 1 = seedling and 2 = vegetative growth.

‡ LSD for the difference between the individual genotypes during the same harvest interval.

§ No significant differences.

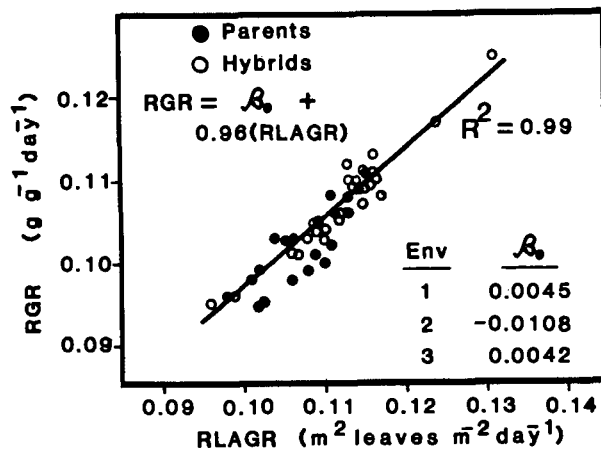


Fig. 3. Relationship between RGR and RLAGR during seedling growth. Symbols represent the predicted values plus the residual model error averaged over environments.

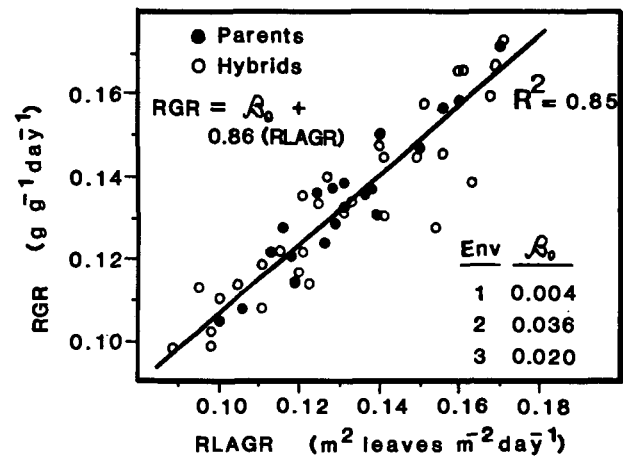


Fig. 4. Relationship between RGR and RLAGR during floral bud development. Symbols represent the predicted values plus the residual model error averaged over environments.

and its parents in either vegetative dry matter or LAI. This lack of difference was probably due to the close genetic relationship between the two parents they used. We took care to select genetically divergent cultivars as parental lines.

The greater total dry matter and LAI of the hybrids was associated with 33, 35, 25, 22, and 43% greater crop growth rates (CGR) for each growth period (Table 2). The last measurement with the greatest CGR values corresponded to the period when substantial vegetative and reproductive growth were occurring simultaneously.

The RGR, RLAGR, and NAR values in the hybrids were generally greater than in the parents for both the seedling and vegetative growth intervals (Table 3). During seedling growth, RGR, RLAGR, and NAR values were 5.9, 6.5, and 5.4% greater, respectively, in the hybrids. These same parameters showed similar trends in the hybrid-parent comparisons during the second harvest interval. No difference in LAP was found among the genotypes during either growth interval. Following the second harvest interval there were

no differences in any of these growth parameters indicating that relative growth advantages (e.g., RGR and RLAGR) of the hybrids were only present during the early stages of growth. Past work on both tomato and maize indicated that the advantages expressed by hybrids manifest themselves during germination and seedling growth and are not related to later growth stages (19).

Muramoto et al. (14) described a close association between leaf area production and dry matter production in several cotton types. We found similar relationships. Subclass regression for the association between RGR and RLAGR occurring during seedling growth interval is shown in Fig. 3. Similar relationships were apparent for all environments. No significant difference was found among the slopes (β_0); however, the y intercept (b_1) was different for each environment. Essentially, changes in dry weight were equal to changes in leaf area. The relationship between leaf area production and dry weight production remained strong as long as concurrent increases in both leaf area and dry weight continued. Figure 4 presents

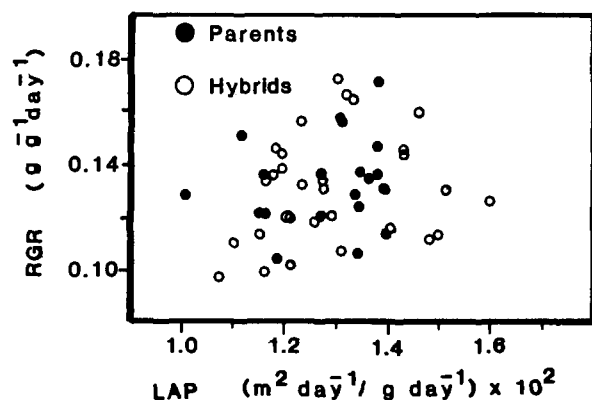


Fig. 5. Relationship between RGR and LAP during floral bud development. The relationship was not significant.

the association between RGR and RLAGR during early reproductive growth. As before, the slope of the regression line is similar but the β_1 values differ among environments. The data suggest that advantages induced by heterosis equally affect the growth rates of leaf area and total dry matter. These relatively small augmentative growth rates can be important in determining final plant weight, because total growth is the end result of factors that influence the exponential nature of plant growth (4). In addition, because cotton is an indeterminate plant, the plant development would be altered by the earlier attainment of ontogenic events. This phenomenon could be the cause of earlier maturing nature of the hybrids as estimated by the percentage of the total lint harvested at the first harvest date (Table 1). Earlier maturing characteristics have been noted in cotton hybrids (20).

The proportion of leaf area produced per unit of dry weight produced was estimated by LAP. Since no difference was apparent among the genotypes, the greater leaf area of the hybrids was not a result of an alteration of the partitioning characteristics, but rather a result of the general augmented growth patterns of the progeny. The weak association between RGR and LAP during early reproductive growth supports this conclusion (Fig. 5). This lack of association is not like that found by Potter and Jones (15) where RGR was closely related to LAP within numerous crop and weed species in response to varying temperatures. These workers provided constant environmental conditions (e.g., temperature, light, humidity) throughout their experiments. Our experiments were conducted in the field where early season environmental conditions became more nearly optimal with time. This is evidenced by the increase in RGR, RLAGR, and NAR during the first two growth intervals. Direct comparison of these two studies is difficult due to these environmental differences.

Unlike RGR vs. RLAGR, the nature of the relationship between RGR and NAR was influenced by the growth environment (Fig. 6). Both the β_0 and the β_1 values differed among the environments; however, the regression proved to be linear in each case. The different slopes indicate that the unit change in RGR per unit change in NAR differed among environments, yet the relationship was linear within an environment. After the first growth period, the association between RGR and NAR was similar among the environments

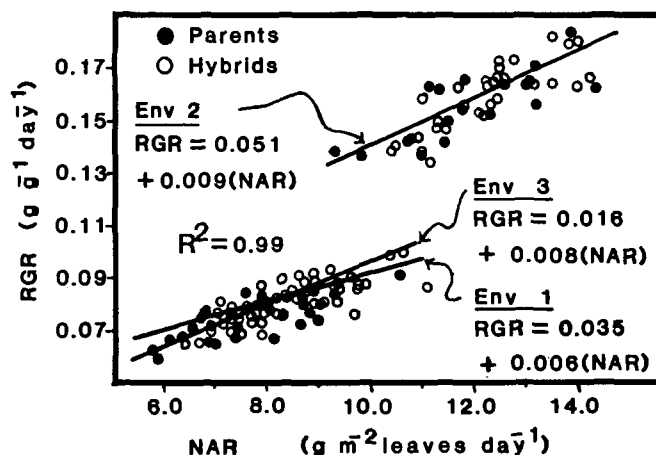


Fig. 6. Relationship between RGR and NAR during seedling growth. Symbols represent the predicted values plus the residual model error.

(data not shown). The greater NAR of the hybrids during early growth suggests a greater photosynthetic rate per unit leaf area. Bhatt and Rao (2) reported a 63% increase over the parental mean in an intraspecific hybrid's sympodial leaf photosynthetic rate. Muramoto et al. (14) and further work at this location (unpublished data) have failed to find increases in hybrid leaf photosynthesis. This lack of significant difference may be due to variation associated with leaf photosynthesis measurements as noted by Mauney et al. (10). Regardless, as Watson (17) states, "it is not safe to assume that all changes in NAR originate from variation in net photosynthesis." Many other physiological processes, including transcription and translation, could be involved in the expression of heterosis at the whole plant level. Greater NAR of the hybrids does not necessarily provide a link between leaf photosynthesis and economic yield, which so many researchers have sought.

The suggestion has been made that species with high leaf photosynthetic rates are likely to be strong competitors in the field (3). Other workers, however, have found that regardless of the photosynthetic rate of a species, true growth potential is enhanced to the greatest extent by leaf area production during early growth (6, 14, 15, 17). The observed heterotic growth of this study, although related to larger leaf area production, does not appear to be a result of greater proportional leaf area partitioning. Instead, the greater LAI seems a product of faster growth of the hybrid progeny during early development and subsequent behavior associated with the exponential nature of the compound interest law (4). Essentially, the final increase in leaf area in the hybrids appears to be a result of the early growth responses.

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