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Potential for Increasing Cotton Yields Through Enhanced Partitioning to Reproductive Structures

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ABSTRACT

Yield increases in cotton (*Gossypium hirsutum* L.) have been primarily through changes in partitioning dry matter from vegetative to reproductive structures. The objective of this study was to determine if yield increases would likely continue through continued changes in dry matter partitioning. Five obsolete cultivars, five popular and high yielding cultivars from five cotton breeding organizations, and 15 advanced strains from five cotton breeding organizations were used for yield and growth analyses at three environments, two in 1985 and one in 1986. Obsolete cultivars averaged 24% less lint than the 20 more modern genotypes and showed greater investment of dry matter into vegetative rather than reproductive structures. There was no major difference in mean yield or growth characteristics detected between the five currently used cultivars and the 15 strains. However, these 20 genotypes showed significant ($P < 0.05$) genetic variability for yield and most growth characteristics. Plant height and stem wt. to total dry wt. ratio showed strong negative genetic correlations with yield ($r = -0.44$ to -0.80). Strong positive genetic associations with yield were found for boll wt. to total dry wt. ratio ($r = 0.86$) and the late sampling of reproductive-vegetative ratio ($r = 0.91$). This study suggests that yield increases through the use of conventional breeding methods are likely to be achieved through continued partitioning of dry matter from vegetative to reproductive structures.

Upland cotton has undergone many genetic changes since its successful introduction about 1810 into the USA from Central America. In its native habitat, cotton was a perennial shrub, required a combination of short days, cool nights, and drought stress for fruiting, had small fruit (2 g seedcotton), and had short dingy brown lint that amounted to about 15% of the seedcotton (Lee, 1984). Modern cotton is grown as annuals, are day neutral in flowering, have large fruit (5–8 g of seed cotton), long coarse to fine-white lint, and a lint percentage of 35 to 40% (Lee, 1984).

Bridge et al. (1971) and Bridge and Meredith (1983) reported that yield gains due to genetic improvement have averaged 10.2 and 9.5 kg ha^{-1} yr^{-1} since about 1910. These yield advances have been accompanied by higher lint percentages, smaller seed and bolls, and higher micronaire values. Wells and Meredith (1984c) indicated that the major component contributing to increased yields was an increase in the number of fruits. This is also in agreement with the explanation of how yield was increased with more but smaller fruits in other major crops (Evans, 1980).

Wells and Meredith (1984b) found that two mechanisms had undergone alteration as a consequence of selection processes aimed towards greater yields. The first was an increased amount of dry matter routed into reproductive growth: greater reproductive/vegetative ratios. The second was the production of a greater proportion of reproductive constituents earlier in plant development. Greater fruit development occurred when leaf area index was maximal; and light, temperature, moisture, and nutrient supply were optimum. Similarly, Hearn (1969) found that faster initiation of fruiting sites and more rapid boll growth rate were associated with greater yield.

The question that confronts cotton breeders is whether further yield increases can be made through reproductive partitioning? Surely, at some point further reductions in leaves and/or stems will not result in improved yields. At that point, yield increases would be obtained only through some other source of variation, such as increased photosynthetic efficiency. The objectives of this study were to determine whether continued genetic yield increases are likely and if so, whether those yield increases will be achieved through enhanced partitioning from vegetative to reproductive structures.

MATERIALS AND METHODS

Twenty five cultivars and advanced strains were grown and evaluated in three environments for yield and growth characteristics. The 25 genotypes chosen represented three groups: five obsolete cultivars, five current cultivars, and 15 advanced strains. The five obsolete cultivars used were Lone Star, Cook 307-6, Deltapine 11A, Deltapine 14, and Coker 100A, whose year of release was 1905, 1917, 1932, 1941, and 1959, respectively. These cultivars, according to Ramey (1966), were involved in the pedigrees of many modern cultivars and breeding programs. The five modern cultivars were McNair 235, Stoneville 825, Coker 315, DES 422, and Deltapine 50. Cotton breeders from five breeding programs were each asked to supply three advanced strains that their research suggested had a good potential of replacing their current cultivars. The only restriction was that the three strains not be closely related to assure genetic variability in the study.

The three environments involved two sites near Stoneville, MS. Tests were conducted on a Dundee silty clay (fine-silty, mixed, thermic Aeric Ochraqualf) with plantings on 17 Apr. 1985 and 25 Apr. 1986. The third test was planted 6 May 1985 on a Beulah fine sandy loam (coarse-loamy, mixed, thermic Typic Dystrochrept). The experimental design was a randomized-complete block with six replications for all three environments. Seed were drill planted at a seeding rate of 20 kg ha^{-1} and then thinned to 10 plants m^{-1} row at about 21 d after planting. Plot size was three rows, each 1 m × 7.5 m. Destructive plant sampling from the outer two rows was made twice from each environment. The average number of days after planting for the earliest sampling was 50 d (range: 47–54 d) and the later sampling averaged 102 d after planting (range: 100–104 d) across the three environments. Because a single harvest required more than 1 d for the whole environment, only complete replications were harvested on any single day. Typically, plant sampling was made on three consecutive days. At each environment the earliest plant harvest was from four plants and the last plant harvest was on three plants from each replication. Yield was

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determined from hand harvest of the middle row. Standard plant growth parameters were recorded (Table 1).

The statistical analysis for genotypic and genotypic × environmental variance, and genetic and phenotypic correlations and computations for genetic advance is the general one used for standard analyses of variance (Miller et al., 1958). The analysis assumes random effects of environments, replications, and genotypes.

RESULTS AND DISCUSSION

The obsolete cultivars yielded 24% less lint than the more modern cultivars (five current cultivars and 15 potential future cultivars) (Table 1), a result that is in agreement with three previous studies, Bridge et al. (1971), Bridge and Meredith (1983), and Wells and Meredith (1984c). Accompanying this selection for increased yield by cotton breeders has been changes in growth characteristics. For the late sampling, significant ($P < 0.05$) differences were detected between the means of obsolete and that of the other 20 cultivars for all growth characteristics except leaf and total dry matter. This trend was also generally evident but was not as pronounced for the early sampling. As in the study by Wells and Meredith (1984a and 1984b), there were no detectable differences in total dry matter produced, but the dry matter was partitioned differently between the obsolete and more modern cultivars. Obsolete cultivars were taller and invested more dry matter into stems, 41%, as compared to 34% for the more modern cultivars at the 102 d after planting (DAP) sample date. On the other hand, the modern cultivars had 48% of their dry matter in bolls as compared to 39% for the obsolete cultivars. The reproductive to vegetative ratio (R/V) was <1 for obsolete cultivars, but >1 for modern cultivars. Thus, cotton has followed the same general trend for yield improvement as that reported by Evans (1980) for other major crops. Genetic yield increases with modern crop management practices have come about through greater partitioning of biomass into reproductive structures. The term used by Evans (1980) for cereal crops is "harvest

Table 2. Genotypic and genotype × environment (gen. × envir.) variance components of 20 modern cultivars (5 current and 15 potential future cultivars) expressed as a percentage of the total of all genetic components† at two sampling dates.

	Early (50 DAP‡)		Late (102 DAP)	
Characteristic	Genotypic	Gen. × envir.	Genotypic	Gen. × envir.
	% of all genetic components			
Lint yield§	28.1**	9.9**	—	—
First fruiting node	16.6**	4.8	—	—
Total node no.	11.7*	13.3**	17.3**	−3.5
Height	18.8**	12.9**	37.7**	−1.3
Internode length	16.6**	2.2	34.7	−0.9
Square no. plant^{-1}	19.0**	12.3**	9.2**	−1.2
Square wt.	11.8*	17.6**	13.2**	−0.4
Stem wt.	2.5	6.0	11.5**	0.6
Leaf wt.	−1.9	11.9**	3.1	−1.6
Boll wt.	—	—	7.8*	11.6**
Reproductive wt.	—	—	7.7*	11.6**
Veg. wt.	—	—	6.4*	−1.1
Total wt.	−0.1	10.2**	2.6*	5.9
Boll no.	—	—	7.3*	12.1**
Square ratio¶	10.8**	−0.2	16.7**	4.7
Stem ratio¶	3.9	7.5*	30.0**	6.4*
Leaf ratio¶	5.1	7.1*	2.6*	8.2*
Boll ratio¶	—	—	20.3**	9.7*
Leaves plant^{-1}	1.2	1.9	−0.4	−3.6
Leaf area index	−1.3	7.2*	2.0	−6.0
Reprod./veg.#	10.5**	−0.4	13.1*	21.1**

*,** Significance of the genotype or genotype × environment mean squares at the 0.05 or 0.01 levels of probability, respectively, as indicated by the *F*-test.

† Total variance components = Genotype × replication (environment) + genotype × environment + genotypic component.

‡ DAP = Average days after planting for sampling for growth characteristics.

§ Total lint yield at end of season.

¶ Ratio of weight of plant trait to total plant dry wt.

Reproductive to vegetative ratio.

Table 1. Average yield and plant growth characteristics at early and late samplings for five obsolete, five current, and 15 potential future cultivars.

	Early (50 DAP†)			Late (102 DAP)		
Characteristic	Obsolete	Current	Future	Obsolete	Current	Future
Yield‡, kg ha^{-1}	870b§	1141a	1142a	—	—	—
First fruiting node	7.4b	6.9a	7.0a	—	—	—
Total node no.	10.1b	9.9a	9.8a	21.2b	19.8a	19.8a
Height, cm	45.6b	44.6a	43.8a	137.8b	124.8a	124.2a
Internode, length, cm	4.5b	4.5b	4.4a	6.5b	6.3a	6.3a
Square no. plant^{-1}	4.9b	5.8a	5.5a	30.3b	11.1a	13.6a
Square wt., g	0.8a	0.9a	0.9a	2.2b	0.9a	0.9a
Stem wt., g	22.6b	23.0b	21.6a	160.2b	141.8a	136.5a
Leaf wt., g	30.5a	30.9a	30.3a	76.8a	72.7a	72.4a
Boll wt., g	—	—	—	170.8b	216.0a	215.9a
Rep. wt., g	—	—	—	173.0b	216.9a	216.8a
Veg. wt., g	—	—	—	237.0b	214.5a	208.9a
Total wt., g	54.0a	54.8a	52.8a	410.0a	431.4a	425.7a
Boll no.	—	—	—	101.6b	113.3a	110.6a
Square ratio¶	0.014b	0.016a	0.16a	0.006b	0.002a	0.002a
Stem ratio¶	0.414b	0.425b	0.406a	0.408b	0.339a	0.335a
Leaf ratio¶	0.572a	0.569a	0.578a	0.197b	0.176a	0.178a
Boll ratio¶	—	—	—	0.389b	0.483a	0.485a
Leaves plant^{-1}	25.0a	26.9a	26.2a	49.9b	49.1b	46.0a
Leaf area index	1.4a	1.4a	1.4a	4.8b	4.6ab	4.4a
Reprod./veg.#	0.014a	0.017a	0.017a	0.80b	1.14a	1.17a

† DAP = average days after planting for sampling for growth characteristics.

‡ Total lint yield at end of the season.

§ Any two means within a row within a sampling followed by the same letter are not considered significantly different at the 0.05 probability level as indicated by the *t*-test.

¶ Ratio of weight of plant trait to total plant dry wt.

Reproductive to vegetative ratio.

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index" and refers to grain to straw ratio. However, cotton is an indeterminate crop and we chose to make genetic comparisons at about 102 DAP since our previous studies (Wells and Meredith, 1984a,1984b) showed that this period would produce the most dry matter. Due to senescence of leaves, later growth stages usually show less dry matter for harvesting than that at about 100 DAP.

There was no difference in yield between the current and potential future cultivars (Table 1). Also, in general there were no major trends in growth characteristics. For example, the R/V's for current and potential future cultivars at 102 DAP were almost identical, 1.14 and 1.17, respectively. A comparison of means might suggest that cotton breeders have reached a plateau in their yield breeding efforts. A closer genetic analysis of variances and genetic correlations however suggests that yield increases are likely to be achieved through further increases in R/V.

For the remaining analyses and discussion, we assumed the five current cultivars and the 15 potential future cultivars would be the foundation for the next yield breeding cycles in the Mississippi River Delta. These 20 genotypes were chosen by five cotton breeders for their potential to produce superior yields. No conscious selection for reproductive partitioning per se was practiced. Significant ($P < 0.05$) genetic variation for yield and most growth characteristics was evident (Table 2). Some exceptions were leaf wt., leaves plant^{-1}, and leaf area index. In general, the genotypic variance was larger in the 102 DAP sample than at 50 DAP, and the genotype × environment component is usually less in the 102 DAP than in the 50 DAP sample. Large genetic differences in plant height and its components node number and internode length were evident. Also, height was a component of stem wt. Stem weight showed significant ($P < 0.01$) genetic variability expressed either on a weight basis (11.5%) or as a ratio to total dry wt. (30.0%) for the 102 DAP sample. Genetic variation in stem and boll amounts is greater when expressed as a ratio than in actual weights. For the 102 DAP sample, the genotype × environment interaction is significant ($P < 0.05$) for all characteristics that have bolls as a component. The R/V showed significant ($P < 0.05$) genetic variation (13.1%) and has a large genotype × environment interaction (21.1%).

Table 3. Genetic and phenotypic correlation coefficients of lint yield with various growth characteristics for two sample dates.

Yield with growth characteristics	Early (50 DAP†)		Late (102 DAP)	
	Genetic	Phenotypic	Genetic	Phenotypic
First fruiting node	−0.04	−0.02	—	—
Total node no.	−0.44	−0.38	−0.32	−0.29
Height	−0.44	−0.34	−0.47	−0.45
Internode length	−0.24	−0.16	−0.29	−0.28
Square no. plant^{-1}	−0.34	−0.18	−0.78	−0.56**
Square wt.	−0.15	−0.12	−0.53	−0.43
Stem wt.	−0.09	−0.25	−0.54	−0.42
Leaf wt.	0‡	0.10	−0.11	−0.33
Boll wt.	—	—	1.04	0.63**
Reproductive wt.	—	—	1.04	0.63**
Veg. wt.	—	—	−0.49	−0.31
Total wt.	0	−0.10	1.01	0.46*
Boll no.	—	—	0.32	0.17
Square ratio§	0.06	0.06	−0.61	−0.48*
Stem ratio§	−0.80	−0.40	−0.77	−0.64**
Leaf ratio§	0.71	0.39	−1.04	−0.36
Boll ratio§	—	—	0.86	0.70**
Leaves plant^{-1}	0.32	−0.00	0	−0.07
Leaf area index	0	0.07	−0.48	−0.18
Reprod./veg.¶	−0.12	−0.07	0.91	0.56**

*,** Significant at the 0.05 and 0.01 level of probability, respectively.
† DAP = Average days after planting for sampling for growth characteristics.
‡ No genetic variance detected in growth characteristic.
§ Ratio of weight of plant trait to total plant dry wt.
¶ Reproductive to vegetative ratio.

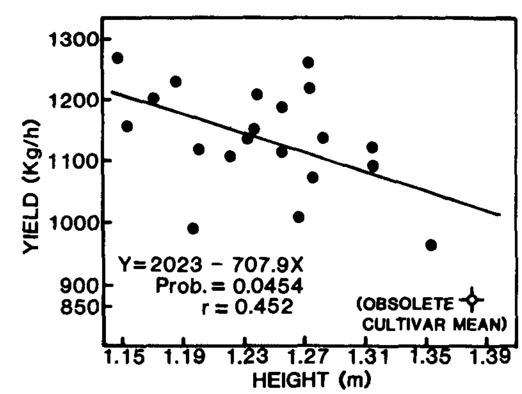

Fig. 1. Regression of yield on plant height from 20 cultivars (5 current and 15 potential future cultivars).

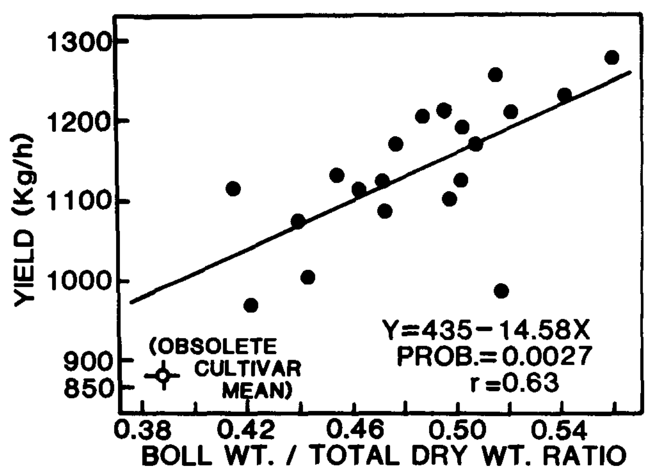

Fig. 2. Regression of yield on boll weight from 20 cultivars (5 current and 15 potential future cultivars).

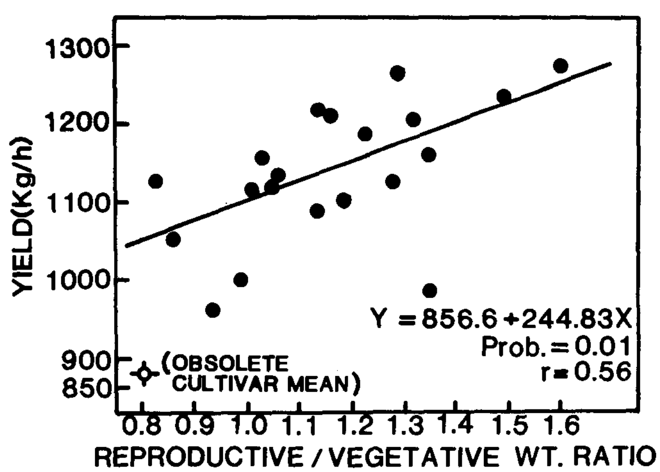

Fig. 3. Regression of yield on reproductive-vegetative weight ratio from 20 cultivars (5 current and 15 potential future cultivars).

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To determine if this genetic variation for growth characteristics can be translated into yield increases, genotypic and phenotypic correlation coefficients with lint yield were computed (Table 3). For the 50 DAP sample, plant height, its component node number, stem wt./total dry matter ratio (S/T) and leaf wt./total dry matter ratio (L/T) showed the highest association with yield. However, none of the 50 DAP phenotypic correlation coefficients were significant ($P > 0.05$). As with genetic variances, the genetic correlation coefficients were usually larger with the 102 DAP sample than the 50 DAP sample. Negative associations with yield at 102 DAP were detected for most vegetative characteristics, but S/T was the only characteristic that showed a significant ($P < 0.01$) phenotypic correlation ($r = -0.64$). In contrast, strong positive associations were detected between boll characteristics and lint yield (Table 3). The negative genetic correlation of yield with square wt. for both 50 DAP ($r = -0.12$) and 102 DAP ($r = -0.43$) samples might not be expected since squares are a part of reproductive growth. For the 102 DAP data, the negative association between yield and square wt. was an indication of a small number of bolls present on high yielding genotypes at the time of sampling and suggest that they will be late in crop maturity. Many studies report that late squares do not translate directly into crop yield. Most of the correlations showed similar trends in both the 50 and 102 DAP samples. One possible exception is L/T with a genetic correlation coefficient of 0.71 for the 50 DAP and -1.04 for 102 DAP. The genetic variances were low, 5.1% for 50 DAP and 2.6% for 102 DAP, but it may be that the correlations also express a need for more leaves early, when leaf area was limiting; and less leaves late in the season, when leaf area was too high. The genetic correlation of yield with R/V was high for 102 DAP, ($r = 0.91$) and suggests that in this sample of genotypes; further partitioning of dry matter to reproductive from vegetative structures is a viable approach to increase cotton yields.

The regressions of yield on height, S/T, and R/V from the 20 modern cultivars are given in Fig. 1, 2, and 3, respectively. Also plotted on these regressions are the means of the five obsolete cultivars, which averaged significantly ($P < 0.01$) less than expected based on the three regression equations. Three possible reasons for this response of the obsolete cultivars include: (i) in early breeding times, the regression coefficient might have been significantly different than that for modern germplasm, (ii) the intercept may be different for obsolete and modern cultivars, and (iii) the true curve may be curvilinear and not simply a linear response. There are many other factors that influence yield besides the three growth characteristics shown. However, they seem to show that there has been a change over time in the linear relationship of yield and some growth characteristics.

One objective of this study was to determine if continued progress through conventional breeding for yield was likely. The genetic variance component for yield among the 20 modern cultivars (5 current and 15 potential cultivars) is large (28%) when expressed as a percentage of the total genetic components (Table 2). This large genetic component suggests that continued yield advances through breeding is likely. A second objective was to determine if this progress would occur through continued partitioning from vegetative to reproductive structures as had been done in past cotton breeding efforts. In the 20 modern cultivars there was a positive genetic association of boll/total dry mater ratio ($r = 0.86$) and R/V ($r = 0.91$) and negative associations of S/T with yield ($r = -0.77$). These associations suggest that at least in the near future yield increases through partitioning from vegetative to reproductive structures is likely to continue. Currently, to our knowledge, cotton breeders do not deliberately introduce R/V variability into breeding programs. However, previously when it became evident that the yield component, lint percentage, was strongly correlated with yield increases, breeders deliberately introduced genetic variability for lint percentage into their breeding programs. For example, Culp and Harrel (1973) indicated that the introduction of the high lint percentage strain C6-5 resulted in increased lint percentage in their breeding program, which led to increased yields. Our study suggests that the addition of useful variability for R/V would likely result in increased genetic advance for yield.

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