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Lint Yield Genotype × Environment Interaction in Upland Cotton as Influenced by Leaf Canopy Isolines[1]

William R. Meredith, Jr.[2]

ABSTRACT

In order to develop a strategy in cotton (*Gossypium hirsutum* L.) for determining the optimum leaf canopy type for each major environment and linking physiology with breeding, the interaction of leaf canopy types with environments was investigated. The lint yield genotype × environment interaction of normal, Okra leaf (L_2^o, L_2^o), and their F_1 and F_2 near-isogenic leaf canopy types of eight cotton cultivars and strains was investigated at Stoneville in 1979 and 1980. The 32 combinations were planted on two dates each year at seeding rates of 9.7, 19.4, and 38.8 seeds m^{-2}. Average yields for the 27 April and 15 May 1979 plantings were 937 and 654 kg ha^{-1}, respectively; the 21 April and 14 May 1980 plantings were 577 and 539 kg ha^{-1}, respectively. Cultivar-strains average yields ranged from 550 to 816 kg ha^{-1}. No leaf type consistently produced highest yields. Average yields of normal, Okra leaf, F_1, and F_2 cotton were 682, 660, 687, and 677 kg ha^{-1}, respectively. Interactions with the four leaf canopy types accounted for 29% of the total genetic variance, whereas interactions with the eight cultivar-strains accounted for 13% of the total genetic variance. Significant negative dominance was detected in 1979 and significant positive dominance was detected in 1980. In 1979, there was a trend for negative compensation in the F_2; the F_2 yielded less than expected based on its three genotypic components. In 1980, there was a trend for positive F_2 compensation. As a result, F_2 leaf canopy types produced the most stable (least variance) yields across all environments and management variables. This study indicates the high interactive effects of leaf canopy types on yield, which are probably linked to leaf canopy types' known association with leaf area and crop maturity.

***Additional index words:* *Gossypium hirsutum* L., Dominance, Compensation, Homeostasis.**

A MODERN strategy for improving crop productivity is to produce the best leaf canopy architecture for each major environment. The Okra-leaf (L_2^o,L_2^o) trait in cotton (*Gossypium hirsutum* L.) confers an open canopy characteristic to the crop. Plant breeders, geneticists, and physiologists have used this trait in their research to develop a more efficient and more productive cotton. Jones (2) reviewed the research on Okra leaf and reported that it reduces individual leaf area by about 35%. Reduced leaf area, in turn, translated into faster fruiting and earlier maturing cotton. This change in one gene pair is also associated with less boll rot, and with resistance to both the banded-wing whitefly [*Trialeurodes abutilonea* (Haldeman)] and the pink bollworm [*Pectinophora gossypiella* (Saunders)]. Okra-leaf cottons are more attractive to tarnished plant bugs [*Lygus lineolaris* (Palisot de Beauvois)] and cotton fleahoppers [*Pseudatomoscelis seriatus* (Reuter)].

Jones (2) reported Okra leaf vs. normal interactions for yield in Louisiana with −3 to 18% more yield for Okra leaf than their normal isolines. In environments where boll rot was a major problem, Okra leaf was higher in yield than normal; where boll rot was not a problem, Okra leaf yields were competitive with normal. In Louisiana environments, Jones (2) reported an average increase in yield of about 5% for Okra leaf over normal. Landivar et al. (3), however, reported an average decrease in yield of about the same magnitude, 5%, and observed genotype × environment interactions for yield between Okra leaf and normal cotton, and concluded that "usually Okra leaf performs comparably to normal leaf in favorable growing seasons, but are worse under adverse conditions." Landivar et al. (3), using the cotton model, GOSSYM, predicted genotype × environment interactions related to moisture stress for Okra leaf, normal, and heterozygous Okra leaf (F_1). Under a moisture regime maintained at field capacity throughout the growing season, their model predicted Okra leaf would produce the highest yields. Under a moisture regime where moderately dry conditions existed from first flowering throughout the remainder of the season, they predicted the F_1 would produce the highest yields. Using four strains with isogenic Okra leaf and frego bract (*fg*,*fg*) combinations, Meredith (4) reported Okra leaf produced 32 kg ha^{-1}, or 4%, more lint yield than normal in a good production year, 1979, but yielded 87 kg ha^{-1}, or 17%, less in a poor production year, 1980.

Little research on the use of intermediate F_1 leaf type or the use of a mixture of leaf genotypes such as the F_2 has been conducted. The objective of this investigation was to measure the genotype × environment interaction of isogenic Okra leaf, normal,

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[2] Research geneticist, USDA-ARS, Cotton Physiology and Genetics, Delta States Research Center, Stoneville, MS 38776.

Table 1. Average yield, first harvest yield, yield components, and plant stand characteristics for the main effects of years, dates, seeding rates, and cultivars-strains.

Variable	Yield Total	Yield 1st harvest	Lint	Boll weight	Seed weight	Lint/seed	Seed/boll	Bolls/plot	Plants/m²
	kg ha⁻¹	kg ha⁻¹	%	g	mg	mg	no.	no.	no.
Year-1979	795**	399**	33.8**	6.15**	122	62**	33.4**	234	11.0**
Year-1980	558	288	32.0	4.36	121	57	25.0	251	9.6
April	757**	408**	33.1	5.48**	122	61**	30.2**	259	7.3
May	597	278	32.8	5.03	120	59	28.2	225	13.3**
$9.7\ m^{-2}$	691	345	33.1	5.43	123	61	29.9	237	5.0
$19.4\ m^{-2}$	676	341	32.7	5.21	121	59	29.0	246	10.6
$38.8\ m^{-2}$	663	343	32.6	5.13	120	59	28.7	244	15.3
$LSD_{0.05}$	NS	NS	NS	0.12	NS	NS	0.6	NS	0.6
DES 24-8ne	816	421	35.6	5.10	111	62	29.5	275	10.7
Coker 201	744	365	34.9	5.21	118	63	28.7	256	9.9
Coker 310	734	386	34.5	5.14	116	61	29.2	257	10.2
Delcot 277	693	392	33.2	5.70	125	62	30.5	222	8.7
PD 2165	656	321	34.0	5.21	122	63	27.9	228	11.1
TH 149	639	286	31.2	5.71	135	61	30.3	227	10.6
Aub 56	583	263	31.3	4.95	120	55	28.3	237	10.1
ORH 55	550	312	28.7	5.04	123	50	29.0	235	11.0
$LSD_{0.05}$†	26	24	0.3	0.11	6	2	0.7	11	0.6

** Indicates significantly greater mean at the 0.01 probability level as indicated by the "F" or synthetic *F tests* for comparisons between years or between months (dates).
† LSD computed from error mean square ignoring any interactions with cultivars and strains.

F_1, and F_2 cottons as influenced by genetic backgrounds, years, and management systems. Also studied were the general relationships of yield components' contributions to yield variations in these studies.

MATERIALS AND METHODS

Four near-isogenic leaf-canopy types were developed from each of six normal leaf cultivars, one germplasm release (DES 24-8ne), and one strain (ORH 55). The four near-isogenic types were normal leaf (*l,l*), Okra leaf (L_2^o,L_2^o), normal × Okra leaf F_1 (L_2^o,l), and the F_2 hybrids, segregating 1:1:2 for the respective genotypes. The six normal leaf cultivars were 'Coker 201', 'Coker 310', 'Delcot 277', 'PD 2165', 'TH 149', and 'Auburn 56'. The six corresponding near-isogenic Okra leaf strains and their recurrent parents were developed by and obtained from Dr. R.L. Shepherd, USDA-ARS, Auburn University, Auburn, AL (7). The germplasm release, DES 24-8ne (5), is a normal leaf cotton in a predominately 'Deltapine 16' background and is also nectariless (ne_1,ne_2). The ORH 55 strain was developed by L.S. Bird, Texas Agric. Exp. Stn., College Station, in his multi-adversity resistance (MAR) breeding program and has both Okra leaf and frego bract characters. Near-isogenic strains of normal and Okra leaf DES 24-8ne and ORH 55 were produced by five backcrosses at Stoneville. Heterozygous (F_1) Okra-leaf seeds were produced by hand crossing in 1978 and 1979 at Stoneville. F_2 seeds were produced from the F_1's at Iguala, Mexico in the 1978-1979 growing season and at Stoneville in 1979 for the 1979 and 1980 research years, respectively.

The 32 near-isogenic leaf type combinations were planted at an early (April) and late (May) planting each year at three seeding rates. The seeding rates were 9.7, 19.4, and 38.8 seed m^{-2}. The planting dates were 27 April and 15 May in 1979 and 21 April and 14 May in 1980. The experiments were planted on a Beulah fine sandy loam (coarse-loamy, mixed thermic Typic Dystrochrepts) soil type. The experimental design was a split-split-split plot with three replications. The two whole plots were planting dates (D), followed by three seeding rates (S), four isogenic leaf types (G), and eight cultivar-strain types (V). All plots of a specific leaf canopy type were grown together and were bordered by that leaf type. Plot size for a sub-sub-subplot was one row 1.02 × 6.1 m long. Furrow irrigation was applied in July of each year.

The yield components, lint percentage, boll weight, seed weight, lint/seed, and seed/boll were determined from 50-boll samples taken from each plot. Yield was determined by hand harvesting the plots. Years, dates of planting, and cultivar-strains were assumed to have random effects and seeding rates and the four leaf canopy genotypes were considered fixed effects.

RESULTS AND DISCUSSION

Two years of testing (Y), two planting dates (D), three seeding rates (S), and eight cultivar-strain backgrounds (V) offer a wide range of environments, management, and genetic variability in which to measure the performance of the four near-isogenic leaf canopies. Average yield and yield components for the main effects of years, planting times, seeding rates, and genetic backgrounds are given in Table 1. Yield is the most important characteristic and all other characteristics are given to relate, in general, how these components of yield were translated into total yield fluctuations.

Average yields were 42% higher in 1979 than in 1980. Plant stands were significantly higher in 1979 than for 1980. About 57% of the seed planted in 1979 produced live plants about 6 weeks after planting, whereas about 49% survival was observed in 1980. Numbers of bolls/plot averaged about the same for both years, 234 vs. 251 for 1979 and 1980, respectively. Lint percentage for 1979 was slightly, but not significantly higher than that for 1980. The component of yield contributing most to the higher 1979 yield was boll weight. Unusually high temperatures in July, 1980 caused some pollen sterility throughout the Stoneville area. This may be the reason why the average boll weight for 1979 (6.15 g) was 41% larger than that for 1980 (4.36 g). Boll weight was larger in 1979 due to 34% more seed/boll and 9% more lint/seed than for 1980. Incomplete pollination in

Table 2. Selected total lint yield variance components expressed as a percent of the total variance involving genotypes and cultivars.

Variance components‡ involving genotypes	df§		Variance components involving cultivars	df	
G	3	0.0	V	7	6.9
Y × G	3	8.0	Y × V	7	11.2**
Y × D × G	3	8.6	Y × D × V	7	1.3*
D × S × G	6	4.4	G × V	21	1.5†
Y × D × S × G	6	7.8*	Y × G × V	21	1.5**

†,*,** Indicates "F" or "synthetic F" test significance at the 0.1, 0.05, and 0.01 probability level, respectively.
‡ All effects listed are assumed to be random except G. G = genotypes, Y = years, D = dates, S = seeding rates, and V = cultivars and strains.
§ df = degrees of freedom.

1980 may have decreased fertilization of ovules, which would decrease seeds/boll and increase lint/seed. In studies on the contributions of yield components to cotton yield, Worley et al. (8) reported results at variance with these. They found that number of bolls/plot was the major determining factor for yield. Boll weight had little effect on yield and lint/seed and seed/boll made positive contributions to increased yield.

The April plantings produced 47% more first harvest and 27% more total yield, 9% larger bolls, 3% more lint/seed, and 7% more seed/boll despite having about 45% fewer plants/plot than the May plantings. Varying seeding rates had little influence on most characteristics. The lowest seeding rate resulted in slightly larger bolls, due to more seed/boll than the other two seeding rates.

The cultivar-strains average yields ranged from 550 to 816 kg ha^{-1} for ORH 55 and DES 24-8ne, respectively. The only detectable trend in seed quality was that Delcot 277 averaged only 8.7 plants m^{-2} or about 44% survival as compared to an average of 10.5 plants m^{-2} or 54% survival for the other cultivars and strains. The linear correlation between stand and total yield, r = 0.23, was not significant. Among cultivars and strains, components of yield that were positively and significantly correlated with total yield were bolls/plot, r = 0.73; lint/seed, r = 0.77; and lint percentage, r = 0.92. Seed/boll and total yield were negatively correlated, r = −0.58.

The primary objective of this study was to measure the effect of four leaf canopies (G) on total yield as influenced by varying management, growing season, and genetic backgrounds. The possible interactions are too many for practical discussion of all combinations. To simplify the discussion, the variance components involving only genetic variables, the main components G and V, and all the 22 interactions involving G or V were totaled. The two main components and the three largest interaction components involving G and V, respectively, are reported as a percent of the total and given in Table 2. Due to the small number of degrees of freedom and large variances associated with variance component estimation, many of the larger components were not statistically greater than zero.

For G, the interactions were such that the effect of G alone was not detectable. The influence of V was more stable, and accounted for 6.9% of the total

Table 3. Average total lint yield and deviations due to dominance and compensation for leaf types grown for 2 years, two planting dates, and three planting rates.

Planting: Year (Y)	Date (D)	Rate (S)	Lint yield: Near isogenic leaf canopies: Norm.	Okra	F_1	F_2	Mean	Deviation due to: Dom.	Comp.
		Seeds m^{-2}	kg ha^{-1}						
1979	Apr.	9.2	968	910	925	879	920	−14	−53
1979	Apr.	19.4	1008	917	945	943	953	−17	−10
1979	Apr.	38.8	944	922	987	901	938	55	−59
1979	Apr.	Mean	973	916	952	908	937	8	−41*
1979	May	9.7	782	808	763	735	772	−32	−44
1979	May	19.4	614	742	670	596	656	− 8	−78*
1979	May	38.8	529	607	476	522	533	−92*	− 0
1979	May	Mean	642	719	636	618	654	−44*	−41*
1980	Apr.	9.7	555	460	628	606	562	121*	38
1980	Apr.	19.4	535	534	609	566	561	72	− 7
1980	Apr.	38.8	572	607	598	649	606	8	55
1980	Apr.	Mean	554	534	612	607	577	68*	29
1980	May	9.7	532	442	526	541	510	39	33
1980	May	19.4	563	445	550	581	535	46	54
1980	May	38.8	584	530	573	609	574	16	43
1980	May	Mean	560	472	550	577	539	34	44*
	Mean		682	660	687	677	677	16	− 2

* Indicates significant "t" test values at the 0.05 level. $LSD_{0.05}$ for comparing isogenic leaf types within a row for a year, date, and seeding rate = 85 kg ha^{-1}, and within a year and date = 49 kg ha^{-1}.

genetic variance. For G, complex interactions of Y × G, Y × D × G, D × S × G, and Y × D × S × G accounted for 28.8% of total genetic variance. For relative comparison purposes, the interactions for V involving the seasonal and management variables, Y × V and Y × D × V, accounted for 11.2 and 1.3%, respectively, or collectively 12.5% of the total genetic variance. These results indicated that the four G isolines were much more sensitive to seasonal and management variability than were the eight cultivars and strains.

Inspection of the variance component estimates for yield components indicated in general no major effect of G. Individual yield component interactions with G were also generally smaller than those for yield. Two exceptions were the interactions of Y × D × S × G for bolls/plot, with 8.9%, and Y × G for stand, with 21.9% of the total genetic variance. The relationship of these components will be discussed briefly in relation to the results given in Table 3.

The largest variance components for lint yield involving G were interactions with Y, D, and S. Table 3 gives the yields of the various combinations of Y, D, and S. Normal cottons were generally more productive than Okra leaf for the 1979-April and 1980-May plantings. Okra leaf produced higher than normal yields for the 1979-May plantings. One method of evaluating the influence of heterozygous Okra leaf (F_1) is to compare the F_1 with the mean of the two homozygotes, normal and Okra leaf. Significant deviations from the homozygotes' mean indicate dominance gene action. Tests for dominance in Table 3 indicated a trend for negative dominance in 1979 and the opposite, positive dominance, in 1980. Over all environments, the F_1 averaged 2.3% more lint than the parental average.

If there is no within-canopy interaction (compensation) among normal, F_1, and Okra leaf plants, the F_2 canopy's expected yield would be equal to the weighted average of its components; $1/4(l,l)$, $1/2(L_2^o,l)$, and $1/4(L_2^o,L_2^o)$, respectively. Table 3 indicates several instances where the observed and expected yields were significantly different. In 1979 there was a trend for negative compensation; the F_2 did not yield as high as expected. In 1980, the trend reversed, and positive compensation was detected. There was also a trend for the F_2 deviation to follow both the direction and magnitude of the dominance deviation. In 10 of 12 cases listed, compensation was in the same direction as the dominance deviation. This suggests that compensation follows the performance of the F_1 plants that account for an expected 50% of the F_2 plants. The formula for estimating compensation in the F_2 generation of these four genotypes is the same as used in a generation mean analysis to detect dominance × dominance epistasis. Working only with normal leaf canopies, Meredith et al. (6) previously used this method to identify significant epistasis in several F_2 hybrids.

Another analysis that summarizes the yield stability of genotypes over varying environments is the stability index of Eberhart and Russell (1). Using the combination of years, dates, and seeding rates to represent 12 random environments, and regressing the genotypes' yield on the environmental yield index, yield regression coefficients (b) of 1.087, 1.054, 0.970, and 0.855 were detected for normal, Okra leaf, F_1, and F_2 canopies, respectively. The regression coefficient for the F_2 is significantly lower than that for each of the other three genotypes; there is no statistical difference among these other regression coefficients. This analysis indicates that the F_2 was the most stable (least variable) genotype in these studies. It produced the highest yields in low yield index environments and the lowest yields in high yield index environments.

The present study shows a high degree of interaction of genotype with environments related to gene substitution at one locus, the L_2^o locus for leaf shape. The interactions involving the two homozygotes and their F_1 and F_2's were greater than those interactions involving eight cultivars and strains, which varied for many genes. The F_1 leaf isolines showed both significant positive and negative dominance that depended on which environment was being sampled. The F_2's showed significant compensation for yield, and tended to follow the direction of dominance. If an F_2 leaf shape population would be more stable in yield, as suggested in these studies, it would offer considerable potential for cotton production in areas with varying environments.

Are the observed interactions, dominance, and F_2 deviations associated with the L_2^o locus typical of what is expected for many other single locus isogenic comparisons, or are these deviations due to this one gene's effect on leaf canopy structure specific for cotton? In his review of leaf morphology mutants of cotton, Jones (2) indicated that the phenotypic effect of changing normal leaf, l,l, to Okra leaf, L_2^o,L_2^o, was a 35% reduction in individual leaf area. This change greatly influences cotton's microclimate. Jones' review (2) indicated that Okra leaf compared with normal leaf allowed greater light penetration into the canopy, resulted in a higher within-canopy temperature, and had a reduced relative humidity within the canopy. This resulted in Okra leaf compared with normal having accelerated fruiting and early crop maturity, less boll rot, and varying sensitivities to insect pests.

Landivar et al. (3) predicted a leaf canopy genotype by moisture regime interaction for cotton yields. In their modeling study, available moisture during flowering and maturation was the only environmental factor being varied; normal cottons were expected to be superior if moisture stress was great; the F_1 was expected to be superior if moisture stress was moderate; and Okra leaf was expected to be superior if moisture was near field capacity throughout the season. In the present study, irrigation was applied and thus prolonged and severe moisture stress did not occur. Based on the implications of Landivar's et al. (3) study, one would have expected the F_1 to produce about 10% more lint than normal leaf and 17% more than Okra leaf. In the field, however, edaphic, climatic, biological, management, and other factors may vary simultaneously. Thus, it should not be surprising that Landivar's et al. (3) modeling expectations based on one variable might deviate from observed field studies.

Cotton is an indeterminate crop, flowering and maturing fruit at Stoneville over a 2-to 4-month period, and thus it is influenced by many environmental fluctuations. It is commonly believed that many genotype × environment interactions are associated with genotypic differences in maturity. Since differences in leaf canopy structure, such as Okra leaf, are known to greatly influence maturity (2), it is likely that the factors causing the observed interactions are also related to maturity.

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