

Agronomic Properties Associated with the Glandless Alleles in Two Varieties of Upland Cotton¹

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ABSTRACT

Experiments conducted at the North Carolina Agricultural Experiment Station showed that, after five generations of backcrossing, glandless strains of upland cotton (*Gossypium hirsutum* L.) yielded from 5 to 10% less fiber than their glandular recurrent parents. Replicated trials involving normal (dimeric), semi-glandless (monomeric), and glandless lines were performed over a period of 3 years at three locations to test the hypothesis that reductions in performance were associated with the glandless alleles. Two varieties were used, and there were four genotypes. In the 'Coker 100-A' varietal background most of the loss in productivity was associated with the gl_2 allele, whereas the gl_3 allele was largely neutral in its effects. Several characters other than fiber yield were affected in some way by the presence of gl_2 . In the 'Empire' background both gl_2 and gl_3 were associated with yield reduction, and gl_2 affected a few other characters. In both varieties gl_2 had much more drastic effects than gl_3 and affected more characters. Although the experiments were not designed to distinguish between linkage and pleiotropic effects, the pattern of the effects suggested that linked factors were the major cause of the loss in performance.

Additional index words: Orthogonal partitioning, Approximate tests, Individual allelic effects.

IN recent years interest has grown in linkage relationships between major alleles and quantitative factors in various crop plants. Much of this interest stems

from two circumstances: (1) failure of the backcross method to restore desired performance after the theoretically required number of generations of manipulation, and (2) as a device for studying the genetical architecture of selected varieties of cultigens. Various workers, notably Fasoulus and Allard (2) and Qualset et al (11) have shown that even small adhering segments of chromosomes can have marked effects on the phenotypes of, otherwise, isogenic lines.

Over the past 7 years we have attempted to transfer the glandless alleles, gl_2 and gl_3 , into adapted varieties of upland cotton (*Gossypium hirsutum* L.) via the backcross method. The experience has been, in general, unrewarding. Testing of glandless material recovered from each backcross generation revealed that little progress was made after the third generation in spite of the fact that some selection for agronomic characters was practiced throughout. After five generations of backcrossing, glandless sibling lines were still yielding from 5 to 10% less fiber than their recurrent parents, depending upon the location of the test. Deficiencies were also noted in lint percentage and boll number per plot. In some lines there were increases in seed size, in others decreases in boll size. In general, glandless lines tended to mature their fruit later than recurrent varieties, so late in fact that they suffered significantly greater frost damage at one station.

It appeared that most of the observed deficiencies in performance were directly relatable to the glandless phenotype. Therefore we designed experiments to determine whether or not relationships between agronomic properties and individual glandless alleles existed.

MATERIALS AND METHODS

Two of the varieties involved in the backcrossing program were 'Coker 100A' and 'Empire 61-WR,' varieties that contrast

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in several ways. The Coker variety tends to mature somewhat later than Empire, and it is usually more productive in North Carolina. It has higher lint percentage, smaller bolls and seeds, and usually grows taller than Empire. On the other hand Empire has among the largest seeds and bolls known in upland cottons, and is very early and determinate in its fruiting habits. We chose these varieties to determine if glandlessness affects contrasting varieties differently.

Following the fifth backcross to the recurrent parental varieties the following genotypes were selected from segregating populations. The method used was developed by Lee (3) and was recently extended to problems in plant breeding by McMichael (8).

Genotype	Phenotype
1. $G_1G_1G_2G_1$	Normally glandular
2. $G_1G_1g_1g_1$	Near normal
3. $g_1g_1G_1G_1$	Sparsely glandular
4. $g_1g_1g_1g_1$	Glandless

For the sake of brevity the alleles were indexed with the following notation as in Lee, Cockerham, and Smith (5): G_1 as a_0 ; g_1 as a_1 ; G_2 as b_0 ; and g_2 as b_1 . The contrast a_0 vs a_1 should detect effects associated with the g_1 allele; b_0 vs b_1 should detect effects associated with the g_2 allele; and the remaining orthogonal contrast estimates the interaction effects between the two loci.

About 12 plants of each genotype were selected and their seed bulked and then increased for field planting. The four genotypes in both varieties were planted in randomized complete blocks at three locations in North Carolina. There were four replications per locations, and the experiment was repeated for a total of 3 years at the same locations. Procedures for laying out performance trials in cotton at the North Carolina Experiment Station have become standardized and need not be repeated here. For a thorough discussion of row length and width, sampling techniques, etc., see Lee, Miller, and Rawlings (6). The following characters were measured.

1. Lint (fiber) yield in kilograms per hectare.
2. Lint percent - the percentage of the unginned cotton that was lint fibers.
3. Boll size - the amount of unginned cotton in grams in a mature fruit.
4. Seed index - the weight in grams of 100 acid-delinted seed.
5. Lint Index - the weight in grams of the lint fibers on 100 seeds. Fewer data were available for this trait than for the others so Lint Index was not entered in tables but is mentioned in the text.
6. Fiber Length - as $2\frac{1}{2}\%$ span length, the percent of the fibers exceeding the length given.
7. Fiber Strength - given as grams per Tex.
8. Fiber Elongation or elasticity.
9. Micronaire - a measure that relates to fiber perimeter.

For a more detailed discussion of the meanings of the various fiber measurements and how they are determined see *The 1965 Book of the American Society of Testing and Material Standards*, Part 25 (11).

Data for the two varieties were analyzed separately and will be presented in that manner. Main effects associated with locations and years, and their interactions, were of no interest for the purposes of this report, and so were excluded. Differences among the phenotypic means of the four genotypes were partitioned into allelic components, orthogonal in error, as follows:

1. Locus a effect = $\alpha_a = \frac{1}{4} (a_1b_0 + a_1b_1 - a_0b_0 - a_0b_1)$
 2. Locus b effect = $\alpha_b = \frac{1}{4} (a_0b_1 + a_1b_1 - a_0b_0 - a_1b_0)$
 3. Interlocus interaction = $I_{ab} = \frac{1}{4} (a_0b_0 + a_1b_1 - a_0b_1 - a_1b_0)$
- where a_1b_1 designate genotypic means.

The genetic effects are presented in Tables 1 and 2. The individual locus effects are defined for each trait as the average effect from replacing a_0 or b_0 alleles with corresponding a_1 or b_1 alleles, or the additive gene effects for the two loci in a randomly mating population with both loci having gene frequencies of one-half. The inter-locus interaction effect corresponds to four times the additive by additive epistatic effect in the same kind of population. The experiment was not designed to detect any of the dominance types of effects. A positive sign denotes a preponderance of expressivity in favor of the g_1 allele and a negative sign greater expressivity associated with the G_1 allele.

Initially, the sums of squares for the interactions of the genetic effects with environments were partitioned into sums of squares due to interactions with "locations," with "years," and with "locations by years" for each of the three effects. In Coker only 1 out of 48, and in Empire 7 out of 48, first order interaction mean squares were significantly greater than the corresponding second order interaction mean square at the 0.05 level. Consequently the corresponding components of variance were assumed to be zero and the three interaction sums of squares pooled for each genetic effect separately to provide "effect \times environment" mean squares. The significance of each genotypic effect was determined by comparing its mean square against the corresponding environmental interaction mean square. This testing procedure was followed in all cases except when the "effect \times environment" mean square was actually less than the general error term. In such cases the "error" mean square was used. This pooling procedure probably alters probability levels somewhat but affords more power for testing than the approximate test outlined by Anderson and Bancroft (1).

RESULTS AND DISCUSSION

Effects Associated with the Glandless Alleles

Except for lint index the genotypic effects for the two varieties are given in Tables 1 and 2 and the interactions of genotypes with environments in Tables 3 through 6. As far as the genotypic effects were concerned the a_1 locus was associated with the greatest amount of disturbance of agronomic traits. Considering first the Coker variety, seven of the nine characters measured were affected in some way. The most drastic effect was upon fiber yield. It was reduced about 12% in the presence of the a_1 allele. Although no systematic boll counts were made in these experiments, estimates indicated that fewer fruits were produced in the plots harboring a_1 . Another important deficit associated with a_1 was inability to produce the crop promptly and relatively early in the season. Plants homozygous for a_1 tended to produce fruit more slowly

Table 1. Phenotypic means of the four genotypes and estimated genetic effects, Coker variety.

Trait	Genotype				Genetic effects		
	$2(a_0b_0)$	$2(a_0b_1)$	$2(a_1b_0)$	$2(a_1b_1)$	α_a	α_b	I_{ab}
Lint yield, kilos/hectare	719.36	669.58	612.91	616.58	-39.86**	-11.53	13.36
Lint percent	37.60	37.53	34.94	34.37	-1.4563**	-0.1604	-0.1229
Boll size	5.96	5.96	6.31	6.28	0.1658**	-0.0092	-0.0092
Seed index	9.07	9.08	9.61	9.33	0.2000*	-0.0612	-0.0708
Fiber length, 2.5% span	1.04	1.05	1.09	1.09	0.0238**	-0.0038	-0.0042
Fiber strength, g/tex.	17.86	17.25	18.21	18.40	0.3750**	-0.1042	-0.2000*
Fiber elongation (E_1)	7.41	7.99	7.66	7.49	-0.0644	0.1006	-0.1906*
Micronaire	4.57	4.65	4.65	4.69	0.0306	0.0306	-0.0115

Simple effects for significant interaction terms:
 Fiber strength (a_0 vs. a_1)/ $b_0 = 0.1750$; (a_0 vs. a_1)/ $b_1 = 0.5750$ **
 Fiber elongation (a_0 vs. a_1)/ $b_0 = 0.1263$; (a_0 vs. a_1)/ $b_1 = 0.2550$ *
 or (b_0 vs. b_1)/ $a_0 = -0.0900$; (b_0 vs. b_1)/ $a_1 = 0.2913$ **

Table 2. Phenotypic means of the four genotypes and estimated genetic effects, Empire variety.

Trait	Genotype				Genetic effects		
	$2(a_0b_0)$	$2(a_0b_1)$	$2(a_1b_0)$	$2(a_1b_1)$	α_a	α_b	I_{ab}
Lint yield kilos/hectare	804.11	773.77	763.22	667.41	-36.81**	-31.53*	-16.37
Lint percent	36.26	36.31	35.77	36.29	-0.1306	0.1417	0.1167
Boll size	8.00	8.07	7.82	7.52	-0.1813*	-0.0588	-0.0921
Seed index	11.64	11.57	11.56	11.43	-0.0563	-0.0500	-0.0146
Fiber length, 2.5% span	1.06	1.03	1.02	1.03	-0.0079*	-0.0033	0.0083*
Fiber strength, g/tex.	18.50	17.50	17.19	17.16	-0.3271*	-0.1646	0.1521
Fiber elongation (E_1)	7.24	7.10	6.98	7.26	-0.0273	0.0352	0.1040*
Micronaire	4.18	4.24	4.26	4.17	0.0031	-0.0110	-0.0350

Simple effects for significant interaction terms:
 Fiber length (a_0 vs. a_1)/ $b_0 = -0.0163$ **;
 Fiber elongation (a_0 vs. a_1)/ $b_0 = -0.1308$ *; (a_0 vs. a_1)/ $b_1 = -0.0767$

Table 3. Mean squares for interaction of genotype with environments for traits associated with lint yield, Coker variety.

Trait		Gen. × Loc.	Gen. × Years	Gen. × Loc. × Yrs.	Error
Lint percentage	α_a	0.81	2.16	0.88	0.550
	α_b	0.41	0.76	1.88*	
	I_{ab}	1.82	0.12	0.73	
Seed index	α_a	0.71	0.23	1.07**	0.259
	α_b	0.39	0.20	0.28	
	I_{ab}	0.13	1.41	0.33	
Boll size	α_a	0.15	0.31	0.03	0.097
	α_b	0.06	0.04	0.06	
	I_{ab}	0.18	0.32	0.07	
Lint yield	α_a	48,850.34**	20,057.14	8,976.81	7,542.62
	α_b	9,001.92	221.25	23,669.19*	
	I_{ab}	21,155.50	297.41	22,457.20	

Table 4. Mean squares for interaction of genotype with environments for fiber properties, Coker variety.

Trait		Gen. × Loc.	Gen. × Years	Gen. × Loc. × Yrs.	Error
Fiber length	α_a	0.0003	0.0006	0.0001	0.0006
	α_b	0.0001	0.0002	0.0034*	
	I_{ab}	0.0001	0.0009	0.0003	
Fiber strength	α_a	0.3419	0.0833	0.1327	0.3434
	α_b	0.4765	0.0209	0.4039	
	I_{ab}	0.1768	0.0342	0.2002	
Fiber elongation (E_1)	α_a	0.2025	0.7180	0.0379	0.1788
	α_b	0.0339	0.0030	0.4757	
	I_{ab}	0.15787	0.2445	0.1263	
Micronaire	α_a	0.0005	0.0011	0.0280	0.0187
	α_b	0.0321	0.0017	0.0185	
	I_{ab}	0.0987	0.0353	0.0408	

Table 5. Mean squares for interaction of genotype with environments for traits associated with lint yield, Empire variety.

Trait		Gen. × Loc.	Gen. × Years	Gen. × Loc. × Yrs.	Error
Lint percent	α_a	1.11	0.47	0.33	0.34
	α_b	0.13	1.22	0.50	
	I_{ab}	0.39	4.41**	0.28	
Seed index	α_a	0.04	0.33	0.01	0.16
	α_b	0.04	0.77*	0.20	
	I_{ab}	0.02	0.06	0.00	
Boll index	α_a	0.12	0.35	0.14	0.086
	α_b	0.27	0.14	0.59**	
	I_{ab}	0.06	0.06	0.16	
Lint yield	α_a	12,039.44*	28,524.08**	20,896.02**	1,869.34
	α_b	37,863.26**	755.19	26,310.71**	
	I_{ab}	7,074.43	29,952.78**	5,982.44	

Table 6. Mean squares for interaction of genotype with environments for fiber properties, Empire variety.

Trait		Gen. × Loc.	Gen. × Years	Gen. × Loc. × Yrs.	Error
Fiber length	α_a	0.0002	0.0002	0.0003	0.0008
	α_b	0.0005	0.0002	0.0007	
	I_{ab}	0.0002	0.0002	0.0011	
Fiber strength	α_a	1.2145	0.5420	1.0018*	0.2189
	α_b	0.3777	0.0020	0.8556	
	I_{ab}	0.6877	0.4237	1.7781*	
Fiber elongation (E_1)	α_a	0.1257	0.1398	0.0474	0.1050
	α_b	0.1459	0.0015	0.0173	
	I_{ab}	0.1012	0.0072	0.1256	
Micronaire	α_a	0.0339	0.0745	0.0434	0.0376
	α_b	0.0005	0.0043	0.0017	
	I_{ab}	0.0411	0.3251**	0.0147	

and a larger proportion of the flowering occurred later in the season. As a result damage from frost and insects was substantially greater, and these agencies seemed to account for much of the reduction in yield. The significant interaction in Table 4 for lint yield was brought about by the fact that at one station the growing season for cotton is somewhat longer than at the other two, and that insect control was better.

Continuing with Coker, lint percent is less for a_1 than a_0 and seed size is greater with a_1 . Frequently seed size and lint percentage are negatively correlated in upland cotton, and the measure of greatest significance is lint index, the actual weight of the fiber on a seed. Lint index is usually more highly correlated with fiber yield than lint percentage. Two years data

on lint index for Coker revealed that lint index in the presence of a_1 was reduced ($\alpha_a = 6.20^{**}$).

In upland cotton there is commonly a correlation between seed index (size) and boll size. In Coker there is a correlated response for increase in both seed index and boll size in the presence of a_1 .

Two of the four fiber properties, lint length and lint strength, were increased in the presence of a_1 . These changes can be viewed as improvements in fiber quality. The improvement in fiber length is rather surprising in view of the very short fiber of the donor strain, Glandless 38-6. We have no data on fiber strength for glandless 38-6 but we suspect that it might have relatively strong fiber, since one of its parents, Hopi-Moencopi, has been used as a source of fiber strength in breeding programs. When the interaction term for fiber strength was broken into simple effects it was revealed that substituting a_1 for a_0 in the presence of b_1 had a significant effect on increasing fiber strength, whereas making the substitution in the presence of b_0 did not. This result may be interpreted to mean that increased lint strength is in some way associated with a_1 , but its expression is partly masked by the presence of b_0 .

Turning to Empire, both a_1 and b_1 were associated with reductions in fiber yield, reducing yield 9 and 8%, respectively. However, they were not cumulative in their effects. Boll size was significantly reduced in the presence of a_1 , but seed size was not reduced. Further a_1 was associated with decreased lint length and strength, the opposite of the effects noted in Coker. There was a small tendency for a_1 to reduce fiber length in the presence of b_0 , as well as a slight tendency to reduce elongation in the presence of b_0 .

In general, Coker was more drastically affected by the presence of the glandless alleles than was Empire. It suffered a greater reduction in fiber yield, lint index, and lint percent. Seed index and boll size showed increases, but these increases are not necessarily agronomically desirable. On the positive side from the agronomic point of view, were increases in lint length and strength. The b_1 allele was largely neutral in its effects in Coker, although it did produce at least one significant genotype × environment interaction.

Although Empire was less drastically affected than Coker, the b_1 allele produced more effects. But this was largely confined to fiber yield.

Empire and Coker were chosen because of their contrasting characteristics, and the evidence strongly suggests that the incorporation of glandless affects them differently. No information can be gained from these experiments as to how glandlessness might affect other varieties of cotton, since variety effects in the current experiments was a fixed quantity. However, comparisons of the current results with information gained from discussions with breeders suggests that fiber yield is likely to be a problem with a broad spectrum of varieties. As for other properties, the fact that Coker and Empire contrasted so sharply in their response to the incorporation of glandless suggests that the outcome of breeding programs could be unpredictable, if backcrossing alone is used.

Linkage or Pleiotropy?

The current experiments were not designed to distinguish between linkage effects and pleiotropy. Yet

being able to make such a distinction could be of crucial importance to a breeder.

It seems rather unlikely that characters such as seed size and boll size should be pleiotropic expressions of glandlessness, although they could be related to reduced fruit number per plant, and thus related to reduced fiber yield. Experiments performed under greenhouse conditions where fruit number per plant were varied by pruning revealed that fruit and seed size are independent of fruit number per plant under those conditions.

The gland-determining alleles, a_0 and b_0 , express themselves in similar ways although their relative levels of expressivity are different (4). The mutant alleles, a_1 and b_1 , on the other hand, combine to remove the glands. There is thus good reason to believe that the genes at these loci have similar functional properties. It follows that if seed and boll size were related to pleiotropic expressions of glandlessness, both a_1 and b_1 should be expected to make a contribution. In fact only a_1 relates to differences in boll and seed size. This result can be interpreted to mean that the relationship between glandlessness and changes in boll and seed size is attributable to linkage and not pleiotropy.

Disturbances in lint percentage and lint index, likewise, seem to be cases of linkage. However, no disturbances were noted in Empire. This could be because of changed linkage relationships or to inherent differences in the genetic makeup of the two varieties, so that the effects on lint percentage and lint index are, in Empire, ameliorated by genes at other sites. Again we have a case where a_1 was effective, this time in only one of the two varieties, whereas b_1 was effective in neither.

As for fiber properties, the contrasts between the two varieties are most striking and unexpected. Increased fiber length and strength could be related to reduced yield in Coker, but this will not answer for the differences noted in Empire. The behavior of fiber properties in the two backgrounds affords no clue as to whether or not linkage or pleiotropy is involved. This example seems to be another case of the unpredictable behavior of the a_1 allele and its accompanying segment in different backgrounds.

Fiber yield represents the sum of the interactions among various yield components and their genetic backgrounds must be very complex. The most important component of fiber yield is fruit number per unit field surface measured. Maximizing fiber yield in North Carolina depends upon having varieties that produce an abundance of bolls in the relatively short season available, that is to say, they must be early in the sense described by Richmond and Radwin (10). In most years, the effective fruition period rarely extends beyond August 10. Any fruit set later than this matures slowly and is subject to frost damage, and is in greater danger of being lost to insects predation. Glandless Coker and Glandless Empire tend to set fewer fruits during July than their glandular recurrent parents. There is a distinct tendency to set fruit toward the cooler end of the season in late August and early September. This could be as a result of an inherent tendency linked to a_1 . This gene is known to have been derived from the Hopi-Moencopi strain of cotton, an ancient, indigenous cultigen from the

plateau region of northern Arizona. Hopi cotton is very late and unproductive in North Carolina, but is described as being early and determinate in its native surroundings (7). It is tempting to speculate that Hopi cotton requires a lower temperature for orderly fruition than is generally available in North Carolina during midsummer, and that this character is at least in part linked to a_1 . The problem needs to be studied in depth. The strongest case for linkage effects as regards disturbances associated with a_1 and b_1 is to be found in the heterogeneous nature of the effects associated with the two alleles over a broad spectrum of traits. This conclusion, of course, assumes that the basic action of the a_1 and b_1 alleles are the same.

Implications in Breeding

It is evident that attempting to introduce glandlessness into adapted upland varieties through backcrossing without attendant selection will only fortuitously result in restored agronomic performance, even if linkage is at the root of the problem. If pleiotropy is the cause of the difficulties, the problem becomes virtually insurmountable through backcrossing (this route) and extremely difficult by any breeding method. Whatever method is used, the low heritability for lint yield on the basis of individual plant estimates makes it necessary that progeny testing be invoked.

Since there is good reason to believe that linkage is involved, the breeder might be wise to proceed with programs designed to change the linkage relationships. Up to a point the backcross method should be used, since the major task in the earlier phases of the program is to set the major features of the recurrent lines on a glandless background. The breeder should familiarize himself with the salient features of the recipient lines, so that he can readily detect any persistent deficiencies that accompany the glandless character from the donor line, or any convergence in the direction of the recipient line. Progeny testing will be of crucial importance in the identification of convergent lines, for if linked genetic blocks are involved in the difficulties, convergence might occasionally be of the "great leap forward" type rather than a stepwise progression through the various traits showing deficiencies. These would be the most desirable kinds to have, but all lines showing ameliorations of "difficult" characters should be saved. Linkage changes in one character might be accompanied by gains in others. For example, alterations in seed size, fruit size, and lint percentage can be detected with single plants, plants that might harbor the potential for increased fiber yield as well. At any rate, lines showing gross convergence are apt to be rare and would be most likely found among lines recognized initially for alterations in one, or perhaps two, characters.

Since a_1 is the allele most likely to be associated with difficulties, one approach would be to deal with it separately. Fortunately the genotype $gl_2gl_2Gl_3Gl_3$ is well marked in *G. hirsutum*, the most outstanding feature of its expression being virtually glandless bolls.

Once convergent lines are selected, the breeder should have few problems in adapting his material to various types of breeding programs. About the only foreseeable problem would stem from the masking of deleterious associated characters by genes elsewhere

in the genome. The differences in response to the incorporation of glandlessness between Coker and Empire could be at least in part due to such masking. Such associations could breakdown when selected lines are used further and the deleterious characters reappear. Unfortunately there is no easy way to distinguish between masking and altered linkage relationships for single characters, so that the problem remains to confront the breeder. However, block losses of characters usually indicate linkage changes and are less likely to be due to masking. Perhaps the best way to guard against unmasking, or to afford the best chance of acquiring or maintaining it, is to maintain a high level of genetic variability in the breeding population, and strive for new combinations (varieties) instead of trying to correct deficiencies in the old ones, varieties which, historically, become obsolete within a few years after their introduction.

LITERATURE CITED

1. Anderson, R. L., and T. A. Bancroft. Statistical theory in research. McGraw-Hill Book Co., New York.
2. Fasoulas, A. C., and R. W. Allard. 1962. Nonallelic gene interactions in the inheritance of quantitative characters of barley. *Genetics* 47:899-907.
3. Lee, Joshua A. 1962. Genetical studies concerning the distribution of pigment glands in the cotyledons and leaves of upland cotton. *Genetics* 47:131-142.
4. ———. 1965. The genomic allocation of the principal foliar-gland loci in *Gossypium hirsutum* and *Gossypium barbadense*. *Evolution* 19:182-188.
5. ———, C. C. Cockerham, and F. H. Smith. 1967. The inheritance of gossypol level in *Gossypium* I. Additive, dominance, epistatic, and maternal effects associated with seed gossypol in two varieties of *Gossypium hirsutum* L. *Genetics* 59:285-298.
6. ———, P. A. Miller, and J. O. Rawlings. 1967. Interaction of combining ability effects with environments in diallel crosses of upland cotton *Gossypium hirsutum* L. *Crop Sci.* 7:477-481.
7. Lewton, F. L. 1912. The cotton of the Hopi Indians; a new species of *Gossypium*. *Smithsonian Misc. Coll.* 60:2146.
8. McMichael, S. C. 1969. Selection for glandless seeded cotton plants. *Crop Sci.* 9:518-520.
9. Qualset, C. O., C. W. Schaller, and J. C. Williams. 1965. Performance of isogenic lines of barley as influenced by awn length, linkage blocks, and environment. *Crop Sci.* 5:489-494.
10. Richmond, T. R., and Sami R. H. Radwin. 1962. A comparative study of seven methods of measuring earliness of crop maturity in cotton. *Crop Sci.* 2:397-400.
11. The 1965 Book of A.S.T.M. Standards. Part 25. The American Society for Testing and Materials, Philadelphia.