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Quantitative trait loci affecting cotton fiber are linked to the t_1 locus in upland cotton

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Abstract Pilose (T_1), a dominant marker in upland cotton, has been associated with coarse, short fibers. Pilose was, thereby, considered to be pleiotropic on fiber fineness and length. However, a pilose-expressing line with a fiber of average fineness was recently identified. This finding does not support pleiotropy between T_1 and fiber traits, but is indicative of linkage between pilose and loci influencing fiber characteristics. To understand the relationship between T_1 and fiber traits, a pilose line with short, coarse fiber was crossed to two t_1t_1 lines with standard fiber characteristics. One hundred and forty-nine F_2-derived F_3 lines were developed from one cross, and 60 F_2-derived F_3 lines from the other. Seven fiber traits (elongation, maturity, micronaire reading, perimeter, 2.5% span length, strength, and wall thickness) were measured. Segregation was normal, as indicated by allelic frequencies of 0.5 for T_1 and t_1, and segregation ratios of 1:2:1 for marker genotypes. The association of homozygous T_1 lines with fibers of average fineness was again observed. Linkage between T_1 and loci affecting micronaire, perimeter, 2.5% span length, strength, and wall thickness was found in both populations. Significant additive and non-additive gene effects for each of these traits at the marker locus were found as well. The pilose marker accounted for 10–75% of the phenotypic variation associated with each trait. In conclusion, the t_1 locus is linked to numerous loci that influence fiber traits, and this linkage has previously been misinterpreted as pleiotropy.

Key words *Gossypium hirsutum* L. · Morphological trait · Additive gene action · Dominant gene action

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Introduction

When obsolete and modern cultivars of upland cotton (*Gossypium hirsutum* L.) were compared, significant improvements in agronomic characteristics (Bridge and Meredith 1983), such as yield, and correlated changes in physiological traits (Wells and Meredith 1984a, b, c), such as greater partitioning of dry matter to reproductive organs, were found. This was not the case for fiber characteristics. With the exception of micronaire (a yield component and measure of fiber fineness), obsolete and modern cultivars were similar (Bridge and Meredith 1983; Wells and Meredith 1984c). This finding was not unexpected, since quantity is rewarded in cotton production, and breeding programs emphasize yield over fiber traits (Meredith 1980). In practice, simultaneous improvements in yield and fiber characteristics also proved difficult to make (Meredith and Bridge 1971; Miller and Rawlings 1967). The reasons for such a lack of progress have been identified as the presence of linkages (Meredith and Bridge 1971; Miller and Rawlings 1967) and pleiotropic effects (Sholl and Miller 1976).

Simpson (1947) suggested pleiotropy existed between fiber traits and pilose (T_1), a morphological marker on the long arm of chromosome six (Endrizzi 1975; Endrizzi and Kohel 1966). Pilose is associated with short, coarse fibers and imparts a heavy pubescence on the vegetative parts of plants (Simpson 1947). The association between pilose and fiber quality has remained intact (Knight 1952; Kohel et al. 1967; Lee 1964 1984) until recently, when a cotton homozygous for T_1 was found to produce fiber with a low micronaire reading (Kloth 1993). Because the undesirable fiber traits can be separated from pilose, pleiotropy is unlikely, and linkage between pilose and quantitative trait loci (QTL) affecting fiber becomes a reasonable alternative (Kloth 1993).

The use of morphological markers, such as pilose, to detect QTL has lapsed – superseded by a variety of biochemical markers. These markers generally avoid the limitations associated with the morphological sort: insuffi-

cient number; an F_2 generation that is uninformative because heterozygotes are masked; and confounding effects that can muddle the relationship between marker and trait. The first limitation condemned morphological markers to neglect, but the later two limitations are not as serious. Heterozygotes are revealed by progeny rows, which simultaneously provide estimates of quantitative traits superior to single-plant measurements. Confounding effects between traits and morphological markers are not guaranteed; T_1 has not been associated with detrimental effects on plant growth and development (Kloth 1993; Lee 1984). Thus, morphological markers can serve to detect QTL that are in close proximity.

Whatever the type of marker, a means of detecting cosegregation of the trait phenotype with the marker is required. The method of choice is interval mapping, which detects QTL between two linked marker loci (Knapp et al. 1990; Lander and Botstein 1989). When there is a paucity of markers, this method is impractical. Two alternatives exist. One alternative is analysis of variance. This approach has identified associations between single markers and traits, and, in comparison to interval mapping, been found to produce the same results (Stuber et al. 1992; Bubeck et al. 1993). Linkage detection based on *F*-tests has one troubling issue: disagreement over the relative importance of Type-I and Type-II error rates (Zehr et al. 1992). This argument has caused the probability level for acceptance of a marker and trait association to be contested, but placed within the range of 0.05 to 0.001 (Bubeck et al. 1993; Edwards et al. 1987; Lander and Botstein 1989). The second alternative recognizes linkage between a marker locus and QTL as a mixture of distributions which have parameters that can be estimated with maximum likelihood. Luo and Woolliams (1993) have devised the most recent algorithm that provides a value for the recombination fraction and the information to estimate gene action (Luo and Woolliams 1993) without bias from recombination frequency (Edwards et al. 1987).

The experiments reported in this article determine if pilose has a pleiotropic effect on fiber traits, and if linkage between the t_1 locus and QTL for fiber traits has been misinterpreted as pleiotropy.

Materials and methods

During the summer of 1990, two pubescent (t_1t_1) inbred lines, Empire (Ballard 1950) and FTA (Culp and Harrell 1980), were crossed with 250-14/2 – a T_1 homozygote with short, coarse fiber that was selected from a population of pilose-expressing plants (Kloth 1993) that Lee (1984) had backcrossed to Empire for five generations. Several plants of each line or cultivar were used to make pollinations. F_1 seed from each cross was bulked and planted in the summer of 1991 to produce F_2 seed. F_2 seed was sent to Mexico, and F_2-derived F_3 lines (F_3 lines) were produced in the winter of 1991–1992 by self-pollinating F_2 plants.

One hundred and forty-nine F_3 lines from 250-14/2 × Empire (250 × EMP) and 60 F_3 lines from 250-14/2 × FTA (250 × FTA) were planted in a randomized complete block with two replicates in the summer of 1992. Five plots of each parent and the F_1 were included in each replicate of the 250 × EMP experiment, and two plots of each parent were included in each replicate of the 250 × FTA experiment. One-row plots, 6.1 m long and spaced 1 m apart were used. Seedlings were thinned to 0.1 m apart.

Genotypes of the progenitors of the F_3 lines were determined by examining 20 plants (10 plants replicate^{-1}) from each line for the degree of pubescence on the leaf. When lines expressed a tomentose leaf phenotype, their capsules were examined for trichomes to be certain that T_1 was present, and not related markers that impart dense pubescence but have no determined effect on fiber traits (Lee 1985).

A bulk sample (40–50 fruits plot^{-1}) was harvested from each plot, and a 15-g sample of lint was sent to Star Lab, Knoxville, Tennesee. Star Lab measured elongation, micronaire reading, 2.5% span length, and strength twice on each sample. Star Lab also performed arealometer measurements twice on each sample from which they calculated maturity, perimeter, and wall thickness of the cotton fiber.

Analysis of variance was done using the Statistical Analysis System (SAS) program (SAS Institute 1985). Cosegregation of the t_1 locus and a quantitative trait phenotype was determined with Proc GLM by partitioning variation due to F_3 lines into variation associated with the marker locus and variation among F_3 lines within the marker genotype. Types of gene action were determined by regressing marker genotype means on the genotype with Proc REG. The error term to test for marker locus effects and gene action was the among F_3 lines, within-marker-genotype mean square. In separate ANOVA, single degree of freedom contrasts were used to test for differences in fiber traits between T_1T_1 F_3 lines. Homogeneity of variances for marker classes was tested using Bartlett's test (Snedecor and Cochran 1967). Genotypic correlations were calculated on a progeny mean basis following the procedure of Mode and Robinson (1959). Product-moment (Pearson) correlations were calculated on an F_3 progeny mean basis using SAS (SAS Institute 1985) Proc CORR.

Recombination frequency (r), and additive and dominance effects between T_1 and quantitative trait loci were estimated by the method of Luo and Woolliams (1993) using a program written in Turbo Pascal, version 7.0 (Borland International[1], Scotts Valley, Calif.). Calculations were done using a homoscedastic model, since variance for marker class trait means were homogenous. LOD scores were calculated from the maximum likelihood for an unconstrained r ($0 \le r \le 0.5$) and r fixed at 0.5. Linkage between t_1 and QTL was considered probable when LOD scores were greater than $\chi^2_{0.05,1}=3.84$. Confidence limits were calculated as described in Steel and Torrie (1960). The proportion of phenotypic variation among families that can be ascribed to quantitative trait loci at a marker (R^2) was calculated by SSMarker/SSFamily (Stuber et al. 1992).

Results

Segregation analysis

All F_3 plants with tomentose leaves had trichomes on the capsule. Therefore, the true T_1 allele was present and not just phenotypically similar alleles without an effect on fiber traits (Lee 1985). Segregation was normal in both populations, as judged by segregation ratios and allelic frequencies. Chi-square tests (2 *df*) for deviation of the pilose marker from the expected segregation ratio of 1:2:1 were non-significant ($P>0.05$) in both populations. The frequency of T_1 and t_1 did not differ significantly ($P>0.8$) from 0.5 in either population.

[1] Mention of a trademark, properietary product, or vendor does not constitute a guarantee or endorsement of this item by the USDA and does not imply its approval to the exclusion of vendors that may also be suitable

Table 1 Means and standard deviations for fiber traits of the pilose (T_1) homozygote 250-14/2, Empire (t_1t_1), the F_1, and F_2-derived F_3 lines ($F_{2:3}$) from 250-14/2 × Empire

Statistic	25Ø-14/2	F_1	Empire	$F_{2:3}$		
				T_1T_1	T_1t_1	t_1t_1
Maturity (%)						
Mean	89.8	80.9	76.1	81.9	81.8	81.1
SD	4.6	2.9	2.4	5.0	4.6	4.3
Micronaire reading						
Mean	5.20	4.32	3.87	4.83	4.44	4.09
SD	0.21	0.36	0.16	0.32	0.33	0.27
Perimeter (μm)						
Mean	50.7	50.3	49.8	53.5	50.5	48.0
SD	2.7	1.8	1.0	2.4	2.2	2.0
Wall thickness (μm)						
Mean	3.21	2.65	2.40	2.88	2.71	2.55
SD	0.18	0.06	0.15	0.19	0.18	0.14
Elongation (%)						
Mean	8.03	7.40	7.56	7.90	7.68	7.49
SD	0.34	0.50	0.35	0.48	0.49	0.49
2.5% Span length (cm)						
Mean	2.24	2.54	2.76	2.26	2.49	2.67
SD	0.12	0.07	0.08	0.07	0.09	0.10
Strength (cN Tex^{-1})						
Mean	18.8	19.0	19.5	18.0	18.7	19.2
SD	0.88	0.64	0.83	0.96	1.02	1.2

Fiber traits

Parental lines were not always statistically different for fiber trait means (Tables 1 and 2). Empire and 250-14/2 had means for fiber perimeter and strength that could not be distinguished. FTA and 250-14/2 had similar means for elongation.

In contrast to their parents, the F_2-derived F_3 lines had significant (P<0.02-0.0001) genetic variance for all seven fiber traits (elongation, maturity, micronaire, perimeter, 2.5% span length, strength and wall thickness) measured. 250×FTA, in comparison to 250×EMP, had 4 times more variability for maturity; twice as much variability for micronaire reading, wall thickness, and strength; and was equal in variability for the traits perimeter, elongation, and length. Genetic variance for each fiber trait was partitioned into variance associated with the marker locus and variance among F_3 lines within the marker class (Tables 3 and 4), and significant variation was associated with the t_1 locus in both populations and for all fiber traits except maturity in 250×EMP and elongation in 250×FTA. When the marker-associated variance was further partitioned into additive and non-additive effects (Table 3 and 4), both types of gene action were found to be significant. Significant variation remained for all fiber traits among F_3 lines in both populations after the variation associated with the marker was removed.

Genotypic and phenotypic correlations were calculated for the fiber traits measured in 250×EMP (Table 5). Phe-

Table 2 Means and standard deviations for fiber traits of the pilose (T_1) homozygote 250-14/2, FTA (t_1t_1), and F_2-derived F_3 lines ($F_{2:3}$) from 250-14/2 × FTA

Statistic	25Ø-14/2	FTA	$F_{2:3}$		
			T_1T_1	T_1t_1	t_1t_1
Maturity (%)					
Mean	92.3	81.2	85.7	83.7	79.5
SD	2.6	6.7	6.3	4.7	4.4
Micronaire reading					
Mean	5.58	3.83	4.91	4.32	3.82
SD	0.15	0.30	0.42	0.36	0.26
Perimeter (μm)					
Mean	51.0	46.6	51.2	48.4	47.4
SD	3.3	1.8	2.1	2.5	2.3
Wall thickness (μm)					
Mean	3.39	2.49	2.98	2.70	2.44
SD	0.08	0.22	0.28	0.20	0.15
Elongation (%)					
Mean	7.75	7.19	7.16	7.16	7.05
SD	0.46	0.38	0.44	0.57	0.54
2.5% Span length (cm)					
Mean	2.17	2.84	2.41	2.70	2.89
SD	0.07	0.13	0.08	0.12	0.12
Strength (cN Tex^{-1})					
Mean	19.0	23.3	21.6	22.3	22.6
SD	0.78	1.2	1.5	1.5	1.7

Table 3 Mean squares from an analysis of variance for wall traits of cotton fiber from F_3 lines of crosses between a pilose homozygous line and normally pubescent varieties

Source	*df*	Maturity	Micronaire	Perimeter	Wall thickness
	250 × EMP				
Marker (M)	2	11.3	8.88***	472***	1.65***
Additive	1	18.3	6.62***	332***	1.39***
Non-additive	1	4.3	11.14***	587***	1.92***
F_3 lines within M (Error a)	146	25.3**	0.3***	6**	0.04***
Residual (Error b)	147	16.9	0.06	4	0.02
	250 × FTA				
Marker	2	278***	7.24***	94***	1.77***
Additive	12	261***	5.08***	38***	1.30***
Non-additive	1	295***	9.39***	150***	2.25***
F_3 lines within M (Error a)	57	35.3***	0.20***	9***	0.06***
Residual (Error b)	57	14.4	0.05	2	0.02

, * Significantly different at 0.01 and 0.001 probability levels, respectively

Table 4 Mean squares from an analysis of variance for cotton fiber elongation, length and strength among F_3 lines from crosses between a pilose homozygous line and normally pubescent varieties

Source	*df*	Elongation	2.5% Span length	Strength
	250 × EMP			
Marker (M)	2	2.56***	1.041***	20.60***
Additive	1	1.86***	0.702***	13.54***
Non-additive	1	3.28***	1.39***	27.88***
F_3 lines within M (Error a)	146	0.31***	0.005***	1.65***
Residual (Error b)	147	0.15	0.001	0.62
	250 × FTA			
Marker	2	0.14	0.546***	6.12***
Additive	1	0.15	0.338***	2.47
Non-additive	1	0.15	0.752***	9.98***
F_3 lines within M (Error a)	57	0.45***	0.008***	3.72***
Residual (Error b)	57	0.15	0.002	0.88

, * Significantly different at 0.01 and 0.001 probability levels, respectively

notypic correlations followed genotypic correlations, with one exception. Perimeter and maturity were phenotypically correlated, but not genetically. Two trends were observed. First, wall traits were positively correlated with each other, but negatively correlated with length measurements and strength; second, length and strength were positively correlated.

Association between the t_1 locus and fiber traits

Two F_3 lines (90PE-133 and 90PE-209), homozygous for T_1, were found to have fiber characteristics unlike those of the typical pilose line. Micronaire readings for 90PE-133 and 90PE-209 were 4.25 and 4.05, respectively (Fig. 1), well below the mean of the T_1T_1 genotypic class (Table 1). The micronaire phenotype is the product of the loci affecting wall thickness and perimeter (Kloth unpublished). 90PE-133 and 90PE-209 had a wall thickness of 2.56 µm. This value was significantly lower (F=15.58, P<0.0006) than that of the remaining families in the T_1T_1 marker class. 90PE-209's perimeter (48.4 µm) was also significantly smaller (F=8.7, P<0.007) than the remaining families in

Table 5 Genetic (above diagonal) and phenotypic (below diagonal) correlations between fiber traits in F_3 progenies from the cross 250-14/2 (T_1T_1) × Empire (t_1t_1)

Trait	Maturity	Micronaire	Perimeter	Wall thickness	Elongation	2.5% Span length	Strength
Maturity	–	0.583**	0.113	0.660**	–0.159	–0.295**	0.04
Micronaire	0.588**	–	0.770**	1.004**	0.451**	–0.848**	–0.600**
Perimeter	–0.380**	0.494**	–	0.713**	0.595**	–0.813**	–0.731**
Wall thickness	0.724**	0.960**	0.356**	–	0.359**	–0.832**	–0.555**
Elongation	–0.049	0.281**	0.340**	0.202*	–	–0.465**	–0.598**
2.5% Span length	–0.189*	–0.736**	–0.659**	–0.680**	–0.317**	–	0.599**
Strength	0.029	–0.413**	0.500**	–0.347**	–0.422**	0.485**	–

*, ** Significantly different at 0.05 and 0.01 probability levels, respectively

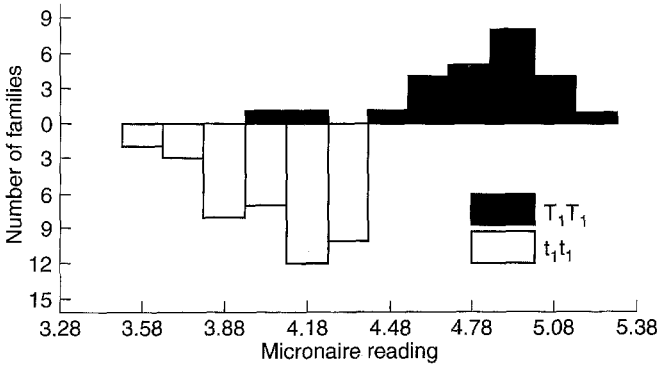

Fig. 1 Histogram of micronaire readings for F_2-derived F_3 lines homozygous for marker classes at the t_1 locus

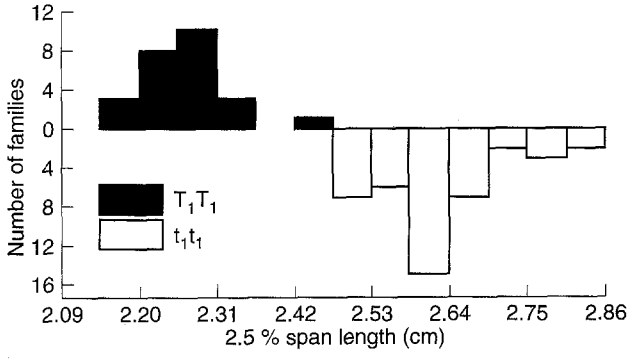

Fig. 2 Histogram of 2.5% span length for F_2-derived F_3 lines homozygous for marker classes at the t_1 locus

the marker class. This line also produced significantly longer (F=19.49, P<0.0002) fiber (2.44 cm, Fig. 2) than the other T_1T_1 lines.

Recombination frequencies were estimated for the six fiber traits that had significant effects associated with the pilose marker (Table 6). Estimated means for the distribution of each QTL genotype and a variance estimate (homoscedastic model) were used to determine estimates for the additive and dominance effects associated with QTL about the pilose locus and 95% confidence interval for the effects (Table 6). Only additive effects for micronaire, perimeter and 2.5% span length had confidence limits that did not pass through zero. No dominance effects, even when doubled to account for half the dominance expressed by an F_3, had a confidence limit that did not encompass zero.

The proportion of the phenotypic variance of each fiber trait that can be associated with the genetic marker was calculated (Table 7). Where linkage was detected, the region surrounding the t_1 locus had a striking effect on phenotype, and the size of the effect was generally comparable between the two populations (Table 6).

Table 6 Estimate of recombination frequency (r), LOD score, and estimates of the additive (add) and dominance (dom) effects with 95% confidence intervals (CI) for fiber traints linked to T_1 in 250 × EMP

Trait	r	LOD[a]	add ± CI	dom ± CI
Micronaire	0.28	63.4	0.39 ± 0.23	−0.05 ± 0.28
Perimeter	0.17	69.0	4.55 ± 2.27	1.14 ± 2.78
Wall thickness	0.34	14.7	0.21 ± 0.31	0.13 ± 0.38
Elongation	0.38	8.7	0.30 ± 0.51	−0.17 ± 0.62
2.5% Span length	0.35	64	0.21 ± 0.06	0.03 ± 0.08
Strength	0.22	20.4	0.77 ± 1.12	−0.27 ± 1.37

[a] Linkage was considered probable when LOD>$\chi^2_{0.05,1}$=3.84

Table 7 Proportion of the phenotypic variance of fiber traits associated with T_1 in two populations

Trait	250 × EMP	250 × FTA
Maturity	0.01	0.22
Micronaire	0.49	0.56
Perimeter	0.52	0.27
Wall thickness	0.37	0.50
Elongation	0.10	0.01
2.5% Span length	0.75	0.69
Strength	0.15	0.05

Discussion

Pilose's pleiotropism (Simpson 1947) became doubtful when a T_1 homozygote with fine fiber was found (Kloth 1993); however, happenstance alone does not provide sufficient evidence to reject pleiotropism. To provide conclusive evidence, the fiber traits of T_1T_1 F_3 lines were compared. Two lines were found with fiber qualities distinct from the T_1T_1 class means but similar to the means of the t_1t_1 lines. The fiber traits affected were different in each line: wall thickness, in one case, and perimeter, wall thickness, and 2.5% span length in the other. The recovery of two T_1T_1 lines with three fiber traits uncharacteristic for pilose-expressing plants makes the pleiotropy hypothesis implausible. Likewise, a hypothesis proposing linkage between pilose and a gene with an epistatic effect on fiber quality is insupportable. Linkage between T_1 and quantitative trait loci which effect cotton fiber is the most likely explanation of the observations. This hypothesis was given additional support when the cosegregation of phenotypes for fiber traits with alleles at the t_1 locus was detected with ANOVA (Table 3 and 4) and maximum likelihood analysis (Table 6). (Significance level of the F-test proved not to be an issue in this experiment, since calculated probabilities fell to either side of the disputed range.)

With the exception of maturity and elongation, the same traits were found to be linked in both populations. Maturity did not segregate with the marker locus in the 250× EMP population (Table 1), nor did elongation in 250× FTA (Table 2). Therefore, at t_1, 250-14/2 and Empire share

alleles with similar effects on maturity, and 250-14/2 and FTA share similar alleles for elongation.

The types of gene action associated with each t_1 trait combination were detected with ANOVA (Tables 3 and 4), and the size of the effect was calculated (Table 6) with the estimate for the trait means at each marker genotype. Only three traits (micronaire reading, perimeter, and 2.5% span length) had additive effects with confidence intervals that did not pass through zero. None of the dominance effects had an error smaller than the calculated effect. Lack of significance may be the result of underestimation by the algorithm. Carbonnell et al. (1993) compared estimates for additive and dominance effects calculated by interval mapping and mixed distribution methods and found the standard errors to be smaller when interval mapping was used. Luo and Woolliams (1993) recognized that their algorithm could underestimate genetic effects. The heritability of a trait, when too low, and the recombination frequency, when over 30%, biased the estimates of the additive and dominance effects (Luo and Woolliams 1993). Fiber traits have heritabilities (Meredith 1984) large enough to avoid underestimation, but recombination frequencies of three of the six traits were greater than 0.3 (Table 6). Therefore, some underestimation of additive and dominance effects for the QTL linked to t_1 is likely.

Despite the errors in estimating the size of gene action, significant additive and non-additive genetic variance was found associated with the t_1 locus (Tables 3 and 4). The detection of significant non-additive genetic variance for fiber traits with every QTL linked to T_1 was surprising. Ramey and Miller (1966) determined additive and dominance variance components for many traits of cotton and found only two dominance variances to be significant – one of which was a measure of fiber fineness, "A". ("A" is measured as the external surface area of fibers of a given volume.) Linkage disequilibrium in the F_2, though very useful in locating QTL, inflates the dominance variance (Moll et al. 1964). There is no doubt that this study and that of Ramey and Miller (1966) have biased genetic variances: both experiments used an F_2 population developed from the crossing of two inbred lines. Therefore, experimental differences are not a satisfactory explanation for an unexpectedly large number of significant non-additive effects. Two factors may have heightened the linkage disequilibrium in the 250×EMP and 250×FTA populations. One factor is the backcrossing of the T_1 allele into Empire. Five generations of backcrossing leaves a significant amount of the chromosome surrounding the locus being transferred intact (Hanson 1959), and, thereby, preserves linkages in the proximity of t_1. The second factor preserving linkages is reduced recombination: the t_1 locus is near the centromere (Endrizzi 1975; Endrizzi and Kohel 1966), where chiasma are generally absent in *G. hirsutum* (Menzel and Brown 1954).

The amount of phenotypic variance for the fiber traits associated with the pilose locus varied from 10% to 75% (Table 7). The highest values resemble the phenotypic variation accounted for when multiple regression methods are used to combine the effect of all marker trait associations (Bubeck et al. 1993; Edwards et al. 1987; Paterson et al. 1991; Schön et al. 1993; Zehr et al. 1992). However, there is not enough data to distinguish between many genes, each affecting a single fiber trait, or a few genes, affecting one or more fiber traits. The genotypic correlations (Table 5) can be interpreted both ways.

The complications of understanding the genetics of the QTL about the t_1 locus, whether the type and size of the gene action or the number of genes involved in the expression of the QTL linked to pilose, can be resolved with three alterations to the experimental design. First, the F_2 generation should be intermated at least once to reduce the linkage disequilibrium (Moll et al. 1964). The lowering of the linkage disequilibrium would help separate linked loci affecting the same trait, determine which loci are closest to t_1, and provide genetic variances with less bias. Second, more markers should be found on chromosome six. A denser map would help locate QTL and separate their effects on fiber traits. Third, population size should be increased to lower the errors associated with the estimates of gene action (Carbonell et al. 1993).

The long-standing, but erroneous, hypothesis of pilose's pleiotropic effect on fiber traits (Simpson 1947) is a testament to the value of marker-based selection. Knight (1952), Kohel et al. (1967), and Lee (1964 1984) backcrossed T_1 into t_1t_1 lines and retained the phenotype of short and coarse fiber in T_1T_1 plants without selection – a demonstration of the ability of marker-based selection to efficiently transfer QTL affecting fiber traits. Meredith (1977 1993) improved the fiber strength of a high-yielding line (without the benefit of markers) by altering the backcross method to include progeny testing for fiber strength. These experiments indicate that backcrossing of desirable fiber traits, especially when bolstered by the efficiencies of marker-based selection, can help overcome the problem of breeding cotton with superior fiber and profitable yields.

In conclusion, loci which influence several quantitative traits of cotton fiber are located on chromosome six in upland cotton. These loci were detected because of their proximity to a locus, t_1, with alleles that have dramatic effects on the distribution and density of trichomes. For one such allele, pilose (T_1), linkage with QTL underlying fiber traits has been misinterpreted as pleiotropy.

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