



Review

Gene effects for cotton-fiber traits in cotton plant (*Gossypium hirsutum* L.) under *Verticillium* conditions

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ABSTRACT

Verticillium wilt (VW), caused by *Verticillium dahliae* Kleb., has become one of the most serious problems in cotton (*Gossypium hirsutum* L.). The use of resistant cultivars has long been considered the most practical and effective means of control. The objective of this work was to study the quantitative genetic basis of fiber traits under *Verticillium* conditions in upland cotton by using five genotypes and their possible crosses without reciprocals, selecting simultaneously for quality fiber, resistance, and agronomic characteristics. Five cotton cultivars and 10 F₁s from half diallel crosses were analyzed for quality fiber under VW conditions. The fiber length, uniformity, strength, elongation, and micronaire were measured during two crop seasons at two different sites each year, consistently in plots with soil naturally infested with *Verticillium*. Genetic components of variance were analyzed using the Hayman model. Analysis of variance for all traits showed significant differences between genotypes, with the genotype–site interaction in most of the studied traits except for fiber length and micronaire. Both the additive genetic variance component (*D*) and dominance genetic variance components (*H*₁ and *H*₂) were present in all traits. *D* was the most important component for uniformity, strength, elongation, and micronaire. Elongation was the trait most correlated with seed-cotton yield. Strength and micronaire were the traits most correlated with VWI. Broad-sense heritability was high for all the traits studied. Narrow-sense heritability was high for uniformity, strength and elongation, and moderate for length and micronaire.

'Acala Prema' and 'Acala Germain-510' were identified as the best parent cultivars to breed for uniformity and strength. 'Acala Prema', 'Acala Germain-510', and 'Deltapine Acala 90' were the best to improve elongation and micronaire characters.

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Abbreviations: VW, Verticillium wilt; VWI, Verticillium wilt index; *D*, additive genetic variance; *H*₁ and *H*₂, dominance genetic variance.

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1. Introduction

Verticillium wilt (VW) in cotton (*Gossypium hirsutum* L.), caused by the soil-borne fungus *Verticillium dahliae* Kleb, is one of the most damaging diseases of this crop worldwide (Bell, 1992). The pathogen infects roots, causing foliar wilt and defoliation. Disease severity depends on several factors, such as the cultivar used, the phenological stage of the plant, environmental conditions, inoculum's density in soil, and the virulence of *V. dahliae* strains (Ashworth et al., 1979; Pullman and DeVay, 1982; Bell, 1992; Bejarano-Alcazar et al., 1995).

In Spain, about 70,000 ha of cotton (*G. hirsutum* L.) are grown annually. Almost 90% of the Spanish production is in the Guadalquivir Valley marsh area (southern Spain), where cotton is grown intensively in clay soil under *Verticillium* conditions (Blanco López et al., 1989). A defoliating pathotype of *V. dahliae* was isolated in 1983 from the soil and later found to be widespread throughout the valley (Blanco López et al., 1989; Bejarano-Alcazar, 2002).

The impact of *Verticillium* wilt on cotton-lint yield depends on the phenotypical stage of the plant when first foliar symptoms appear in the crop (Misaghi et al., 1978). If the first foliar symptoms of VW appear at the end of the growing season, when the cell walls of the individual fibers are fully developed, the main results are lower micronaire and lint weight per boll. One indication of this is the micronaire response of resistant and susceptible cultivars under *Verticillium* conditions. Susceptible cultivars can drop three points (0.3) or more below the micronaire of tolerant varieties (Bassett and Kerby, 1996).

Improvements in textile processing, particularly advances in spinning technology, have led to increased emphasis on breeding cotton for both improved yield and improved fiber properties (Meredith and Bridge, 1972; Green and Culp, 1990; Patil and Singh, 1995). Cotton-lint quality is expressible by a multitude of measurements, including fiber length, uniformity, strength, elongation, and micronaire (Hake et al., 1996). The fiber quality affects different processes of textile manufacture: an excessive percentage of short-fibers augments manufacturing waste; lower yarn strength increases the difficulty of spinning fine-count yarns and can cause fuzzy yarn and other imperfections; low micronaire is more likely to form neps in the ginning and yarn-manufacturing process, causing yarn breakage and defects in end products (Bassett and Kerby, 1996; RAEA, 1999). High micronaire also has limited use in the textile industry because it cannot be spun efficiently into fine yarns (RAEA, 1999).

An objective in the development of new cultivars has been to improve the basic properties of cotton. Like all agricultural commodities, the value of cotton lint responds to fluctuations in the supply and demand forces of the marketplace (Moore, 1996). In addition, pressure toward specific improvements in cotton-fiber quality (for example, the higher fiber strength needed for today's high-speed spinning) has been intensified as a result of technological advances in textile production and imposition of increasingly stringent quality standards for finished cotton products. Changes in fiber quality requirements and increases in economic competition on the domestic and international levels have resulted in fiber quality becoming a value determinant that is equal to fiber yield (Ethridge, 1996; Hudson et al., 1996).

Retaining the fiber quality that is inherent in the genetic traits of the plant can also be an approach to improve fiber properties

(Yankey, 1999). The variation in a fiber trait through plant-breeding approaches requires knowledge of the cultivar's genetics. Supporting information, though limited, is available on the mode of gene action of cotton-fiber traits (Tawhid and Myers, 1999). Studies on gene action suggest that, within upland cotton genotypes, there is little non-additive gene action in fiber length, strength, and fineness (Meredith and Bridge, 1972). However, strong interactions between combined annual environmental factors (primarily weather), fiber strength, and also micronaire suggest that environmental variability can prevent full realization of the fiber quality potential of a cotton genotype (Green and Culp, 1990).

The availability of cultivars resistant to VW is fundamental for the sustainability of the crop. Therefore, looking for genotypes with resistant to *V. dahliae* in world collections of *G. hirsutum*, and studying the genotype variability for the characters related to fiber quality and yield under *Verticillium* conditions are vital issues for a breeding program intended to improve resistance.

The present diallel study was conducted to assist the breeding of fiber quality in cotton under *Verticillium* conditions. A considerable number of diallel studies have been reported in cotton for both of the tetraploid cultivated species (*G. hirsutum* and *G. barbadense*) (Luckett, 1989; Verhalen et al., 1971). Some studies (Bourland and Bird, 1983; Carvalho et al., 1995; Luckett, 1989; Verhalen et al., 1971) have used the Jinks–Hayman analysis method (Hayman, 1954a,b, 1963; Jinks and Hayman, 1953). The Hayman analyses show genetic trends (Hayman, 1954a,b). This information allows breeders to use improved strategies to develop more efficient selection methods. The objectives of the present work were: to study parental genetic behavior, inheritance, the different genetic components, broad- and narrow-sense heritability, and the relation between fiber traits and the resistance to VW.

2. Materials and methods

2.1. Genetic material

F₁ crosses without reciprocals (half diallels) were made by crossing five cultivars of cotton: 'Ma del Mar', 'Victoria' (both Spanish cultivars with early maturity and susceptible to *V. dahliae*), 'Acala Germain 510', 'Acala Prema' and 'Deltapine Acala 90' (characterized by late maturity and tolerant to *V. dahliae*). The parents were self-pollinated in an experimental farm at La Rinconada, Seville (southern Spain).

2.2. Field trial

Field trials were carried out at four sites in the Lower Guadalquivir Valley (Lebrija, southern Spain), for 2 years, two sites each year. In these fields, vertic soils (61% clay, 0.9–1.4% organic matter, pH 8.3–8.8) were naturally infested with quite different inoculum densities of a defoliating pathotype of *V. dahliae* (Aguado et al., 2008).

The plots were arranged in a randomized complete-block design with four replicates at each location. The assays were designated as A and B in the first year and C and D in the second one. Each plot consisted of a single row 10 m long with 95-cm row spacing. In an effort to avoid border effects, 1.5 m at the beginning and at the end of each row was not evaluated.

Plant-stand density was 120,000 plants/ha. Conventional practices for annual cotton production were followed. Plants were hand harvested the 3rd and 7th of October in the first and second seasons, respectively.

2.3. Description of characters

After mechanical ginning, fiber length and other fiber properties were determined with the High Volume Instrument system (HVI Spin-Lab, SL-900) (Moore, 1996). The HVI fiber-length data were converted into percentages of the total number of fibers present at each length value and into other length parameters, such as mean length, upper-half mean length, and length uniformity (Behery, 1993). Fiber length (length), in mm, was reported as the upper-half mean length (UHM, mean length of half-set sample that contains larger fiber). The fiber-length–uniformity index (*uniformity ratio*) is the ratio between UHM and mean length expressed as a percentage of the longest length. Fiber strength is reported as *breaking tenacity* or grams of breaking load per tex, where tex is the fiber linear density in grams per km. Fiber elongation (elongation) as a measurement of fiber extension until its breaking by percentage of the initial length. Micronaire, an indirect estimate of fiber fineness and maturity level, is based on the air-permeability of a test specimen of known mass enclosed in a container of fixed dimensions (RAEA, 2005).

The severity of VW on plants was assessed on the 11th of September in the first year and the 23rd of September in the second year. Disease severity (VWI) and seed-cotton yield were determined as shown in a previous study (Aguado et al., 2008). Disease severity was determined by a VW visual symptoms index (VWI) scaled from 0 to 5, according to the percentage of plant tissue affected by acropetal necrosis, wilt, and/or defoliation: 0–1 = total leaf loss; 1–2 = leaf loss and/or 75–50% or more leaves with strong wilt symptoms or chlorosis; 2–3 = leaf loss and/or 25–50% leaves showing strong wilt symptoms or chlorosis; 3–4 = leaf loss and/or less than 25% leaves showing strong wilt symptoms or chlorosis; and 5 = no symptoms (modified from Bejarano-Alcazar et al. (1995)).

The relationships between fiber traits and seed-cotton yield and disease severity (VWI) were studied in this work.

2.4. Statistical analysis

A combined ANOVA with site as the main factor (SAS Institute, Inc., Cary, NC, USA) was performed for all fiber traits and an ANOVA by site for fiber uniformity, fiber strength and fiber elongation. Conformity of data to the main assumptions (normality of distribution of the error terms, adequacy of the model and homogeneity of residual variances) of the analysis of variance was checked. Mean values of characters for the parental lines were conducted using the LSD test at $P < 0.05$ and $P < 0.01$. Data are presented as means for each genotype.

The correlation between different fiber traits was determined using Pearson correlation coefficients (SAS Institute, Inc., Cary, NC, USA). The traits used were:

- (1) fiber length,
- (2) fiber uniformity,
- (3) fiber strength,
- (4) fiber elongation,
- (5) micronaire.

The values of direct effects of fiber traits on seed-cotton yield and VWI were determined by path-coefficient analysis, allowing the partition of the correlation coefficient, r_{ij} , into direct and indirect effects. The following sets of simultaneous equations were

solved to determine the path-coefficient, P_{ij} (with subscripts indicating the characters) (García del Moral et al., 2003):

$$r_{14} = P_{14} + r_{12}P_{24} + r_{13}P_{34}$$

$$r_{24} = P_{24} + r_{12}P_{14} + r_{23}P_{34}$$

$$r_{34} = P_{34} + r_{13}P_{14} + r_{23}P_{24}$$

In the equation $r_{14} = P_{14} + r_{12}P_{24} + r_{13}P_{34}$, P_{14} is the direct effect of trait 1 on trait 4. Similar definitions are applied to the rest of equations (García del Moral et al., 1991).

The Hayman diallel analysis (Hayman, 1954a,b) was used to evaluate traits that varied significantly among parents. This analysis was carried out by years, including sites A and B in the first year and sites C and D in the second year. This additive/dominance genetic model is based on the following assumptions: (1) diploid segregation (Endrizzi et al., 1985); (2) parental homozygosity; (3) no reciprocal differences (White and Kohel, 1964; Al-Rawi and Kohel, 1969, 1970); (4) independent effect of non-allelic genes (i.e. no epistasis); (5) no multiple allelism; and (6) independent gene distribution. The assumptions 4, 5, and 6 were analyzed by the t -test of uniformity on the difference between W_r (the covariance of hybrids in an array with the recurrent parent) and V_r (the variance of an array), and by the regression coefficient of W_r/V_r (b). Genetic components and parameters may be estimated even though a trait has not completely fulfilled the assumptions of analysis (Hayman, 1954a,b). However, the estimations made under such circumstances are not as accurate as they would have been had all the assumptions were fulfilled.

Significant differences in phenotypes were assumed to imply that genetic differences were present. Genetic components of variance (D , H_1 and H_2) and genetic proportion ($(H_1/D)^{1/2}$) were estimated using the simple additive/dominance model proposed by Hayman (1954a,b). D was the additive genetic variance, and H_1 and H_2 were the components of the variance due to the dominance effects of genes. The F component is an indicator of the relative frequency of the dominant to recessive alleles in the parents. The genetic parameter $((H_1/D)^{1/2})$ is the average degree of dominance among all the loci. The information on gene action was inferred by plotting the variance (V_r) of each array against its covariance (W_r).

Broad- and narrow-sense heritability (H^2 and h^2 , respectively) were calculated according to Mather and Jinks (1982)

3. Results

3.1. Inoculum density

The estimation of the *V. dahliae* population in soil as propagule number per gram of soil (p/g) indicated that plots of sites A (24 p/g), B (24.5 p/g), and C (18.5 p/g) were heavily infested with the pathogen, whereas the soil of site D (7 p/g) was only slightly infested. All the isolates of *V. dahliae* were of the cotton-defoliating type (Aguado et al., 2008)

3.2. Parental differences

Results of combined analyses of variance on fiber length, uniformity, strength, elongation, and micronaire together with the analysis of variance by sites for uniformity, strength, and elongation showed that the genotype effect was significant (Tables 1a and 1b). Since for length, micronaire, and VWI the [site \times genotype] interaction was not significant, a combined ANOVA was performed with site as the main factor, followed by an

Table 1a

Combined analysis of variance in fiber traits under *Verticillium* conditions at four different sites in the Lower Guadalquivir Valley (Lebrija, southern Spain).

Characters	Source of variation	df	MS ^a	P
Length	Sites (S)	3	20.01	0.0000***
	Blocks (B)	3	2.67	0.0000***
	Genotypes (G)	14	3.90	0.0000***
	S × G	42	0.51	0.0640NS
	Error	177	0.40	
	Total	240		
Uniformity	Sites (S)	3	63.38	0.0000***
	Blocks (B)	3	0.68	0.5610NS
	Genotypes (G)	14	21.65	0.0000***
	S × G	42	1.78	0.0020***
	Error	177	0.92	
	Total	240		
Strength	Sites (S)	3	22.38	0.0000***
	Blocks (B)	3	2.99	0.4400NS
	Genotypes (G)	14	64.63	0.0000***
	S × G	42	5.35	0.0190***
	Error	177	3.33	
	Total	240		
Elongation	Site (S)	3	343.09	0.0000***
	Blocks (B)	3	0.036	0.6070NS
	Genotypes (G)	14	3.37	0.0000***
	S × G	42	0.29	0.0000***
	Error	177	0.06	
	Total	240		
Micronaire	Site (S)	3	4.18	0.0000***
	Blocks (B)	3	0.23	0.1700NS
	Genotypes (G)	14	1.19	0.0000***
	S × G	42	0.16	0.2600NS
	Error	177	0.14	
	Total	240		
VWI ^b	Site (S)	3	3.26	0.0000***
	Blocks (B)	3	0.20	0.5100NS
	Genotypes (G)	14	6.31	0.0000***
	S × G	42	0.29	0.3190NS
	Error	177	0.26	
	Total	240		

NS, non-significant at $P < 0.05$.

*** $P < 0.001$.

^a Mean squares.

^b Verticillium wilt index.

LSD test to rank the parental means for all characters (Table 2a). The [site × genotype] was significant for uniformity, strength, and elongation, so that parental mean values were calculated for each site (Table 2b).

Table 1b

Analysis of variance in uniformity, strength, and elongation under *Verticillium* conditions at four different sites in the Lower Guadalquivir Valley (Lebrija, southern Spain).

Character	Source of variation	df	Sites							
			A		B		C		D	
			MS ^a	P	MS ^a	P	MS ^a	P	MS ^a	P
Uniformity	Genotypes (G)	14	7.74	0.0000***	8.32	0.0000***	7.27	0.0000***	3.66	0.000***
	Blocks (B)	3	1.63	0.1900NS	0.09	0.97NS	0.44	0.5000NS	1.14	0.28NS
	Error	42	0.99		1.25		0.55		0.87	
	Total	60								
Strength	Genotypes (G)	14	22.29	0.0000***	24.23	0.0000***	18.55	0.0000***	15.60	0.000***
	Blocks (B)	3	0.51	0.9200NS	1.66	0.8300NS	1.41	0.4100NS	17.26	0.000***
	Error	42	3.30		5.73		1.44		2.32	
	Total	60								
Elongation	Genotypes (G)	14	5.76	0.0000***	0.51	0.0060***	32.26	0.000***	1.33	0.000***
	Blocks (B)	3	2.39	0.0080***	0.01	0.9900NS	1.29	0.29NS	0.12	0.24NS
	Error	42	0.04		0.036		0.06		0.08	
	Total	60								

NS, non-significant at $P < 0.05$.

*** $P < 0.001$.

^a Mean squares.

Average values for parental traits are displayed in Tables 2a and 2b. The data showed that 'Acala Prema' had the highest values for all the traits studied except for micronaire. 'Acala Germain 510' and 'Deltapine Acala 90' presented the highest values for micronaire. The early-maturing cultivars ('Ma del Mar' and 'Victoria') were less tolerant to VW than were the American ones.

3.3. Phenotypic correlation and path analysis

Pearson correlation coefficients for the relationship between fiber traits are shown in Fig. 1. Elongation showed a positive and significant correlation with uniformity, strength and micronaire. Micronaire showed a positive and significant correlation with uniformity and elongation. The Pearson correlation coefficient was significant and positive between length and uniformity at all sites, whereas the correlation between length and elongation was positive and significant at two sites (B and C). Micronaire showed a negative and significant correlation with strength and length at one site each (B and D, respectively), but a positive correlation with strength at site C.

The path-coefficient analysis allowed quantification of the influence of each fiber trait on seed-cotton yield and VWI (Fig. 1). Elongation had the strongest positive and significant direct effect on seed-cotton yield at all sites. Length showed a positive and significant effect on seed-cotton yield in three sites (A, B and C). Micronaire showed a positive and significant effect in two sites (C and D). Two traits, strength and uniformity, had a negative direct effect on seed-cotton yield.

VWI had the strongest positive and significant direct effects on strength and micronaire in three sites (A, C and D). VWI had a non-significant effect on fiber length and uniformity (Fig. 1).

3.4. Diallel analysis

The *t*-test of uniformity on the difference between W_r and V_r showed that the additive/dominance genetic model was adequate for most of the traits studied, with only the *t*-test for $b = 0$ showing no significance for strength in the first year and length in the second year. The *t*-test for $b = 1$ was significant for strength in the first year. Other assumptions were fulfilled by these traits (Table 3 and Fig. 2).

Genetic components estimated by the diallel analysis for length showed that the additive genetic variance (*D*) and components of dominance (*H1* and *H2*) were significant in both years, with similar values for these components in first year. Meanwhile, in the

Table 2a
Mean average values of length and micronaire in parents, in a combined analysis.

Genotype	Length	Micronaire	VWI ^a
'Ma del Mar'	28.93	3.09	1.25
'Victoria'	29.09	3.27	1.50
'Acala Prema'	29.95	3.74	3.03
'Acala Germain 510'	28.59	4.08	3.15
'Deltapine Acala 90'	28.79	3.91	2.93
LSD _{0.05} ^b	0.88	0.52	0.36

^a Verticillium wilt index.

^b Least significant difference (LSD) between genotypes at $P < 0.05$.

second year, the dominance effects were greater than the additive component. The average degree of dominance at each locus ($(H1/D)^{1/2}$), was nearly 1 in the first year and higher than 1 in the second one, confirming complete dominance for this trait. Broad-sense heritability (H^2) was high in the first year and moderate in the second. Narrow-sense heritability (h^2) was moderate for this trait in the first year and low in the second year (Table 4). The regression line intercept Wr axis below the origin (a) in both years confirmed the tendency toward overdominance from this trait (Fig. 2). The values for the correlation (r) between ($Wr + Vr$) and mid-parent (y) for length were negative in both years, indicating that dominant genes could increase this trait (Fig. 2).

Results for uniformity (Table 4) showed that additive and dominance components were significant in both years. The additive effect was greater than the effect of the dominance component. The significant and positive value of F for uniformity in the second year indicated an excess of dominant alleles with dominant effects on the parents. The genetic parameter ($(H1/D)^{1/2}$) value below 1, confirmed partial dominance for this trait. Uniformity showed high values of H^2

Table 2b
Mean average values of uniformity, strength, and elongation in parents.

	Genotypes	Site A	Site B	Site C	Site D
Uniformity	'Ma del Mar'	82.20	82.75	81.90	83.48
	'Victoria'	81.47	82.42	82.12	85.35
	'Acala Prema'	85.07	86.62	86.57	86.73
	'Acala Germain 510'	82.40	85.65	85.10	86.90
	'Deltapine 90'	82.62	84.97	84.57	86.30
	LSD _{0.05} ^a	1.42	1.74	1.06	1.33
Strength	'Ma del Mar'	31.02	33.42	30.57	31.18
	'Victoria'	30.37	31.62	31.35	35.50
	'Acala Prema'	36.17	39.07	36.72	39.95
	'Acala Germain 510'	33.87	35.32	33.82	34.85
	'Deltapine 90'	32.97	33.52	32.70	33.83
	LSD _{0.05} ^a	2.59	3.42	1.72	2.17
Elongation	'Ma del Mar'	5.25	5.15	8.40	8.58
	'Victoria'	5.25	5.05	8.55	9.25
	'Acala Prema'	5.92	6.15	10.65	10.43
	'Acala Germain 510'	5.77	5.82	10.50	10.55
	'Deltapine 90'	5.92	6.00	9.8	10.60
	LSD _{0.05} ^a	0.30	0.27	0.36	0.41

^a Least significant difference (LSD) between genotypes at $P < 0.05$.

and h^2 in both years. The regression line and Wr axis crossed point were over 0 in both years, revealing that the dominance was partial (Fig. 2). Negative correlation (r) between ($Wr + Vr$) and mid-parent (y) in both years indicated that the dominant genes were responsible for this trait variation (Fig. 2).

Genetic components estimated by the diallel analysis for strength showed that the additive component (D) and dominance ($H1$) were significant for both years. Meanwhile, dominance ($H2$) was significant only for the second year. The additive component

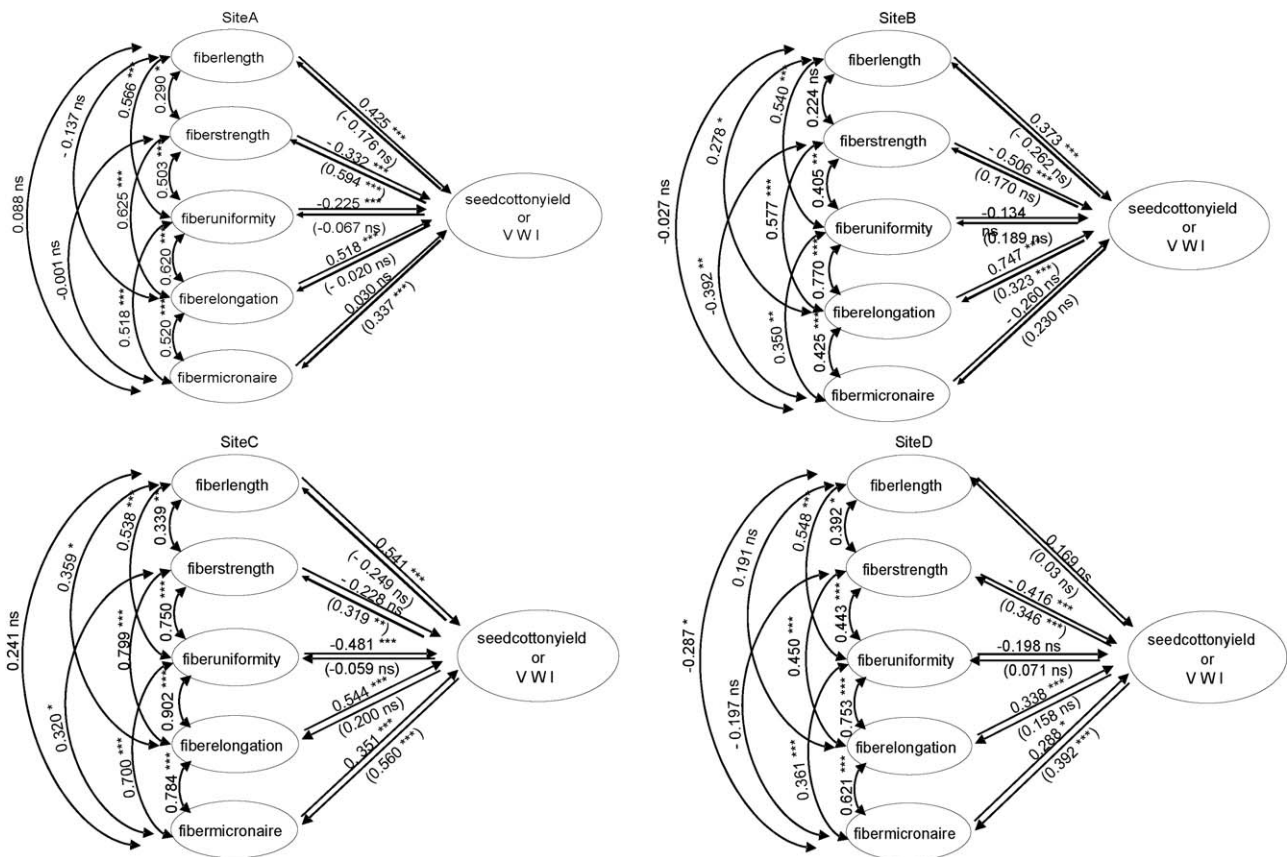


Fig. 1. Path-coefficient diagram showing the interrelationships between cotton-quality traits and seed-cotton yield or Verticillium wilt intensity (VWI) by sites. The single-headed arrows indicate path-coefficients both for seed yield (naked values) and for the VWI (values between brackets), whereas double-headed arrows indicate simple correlation coefficients.

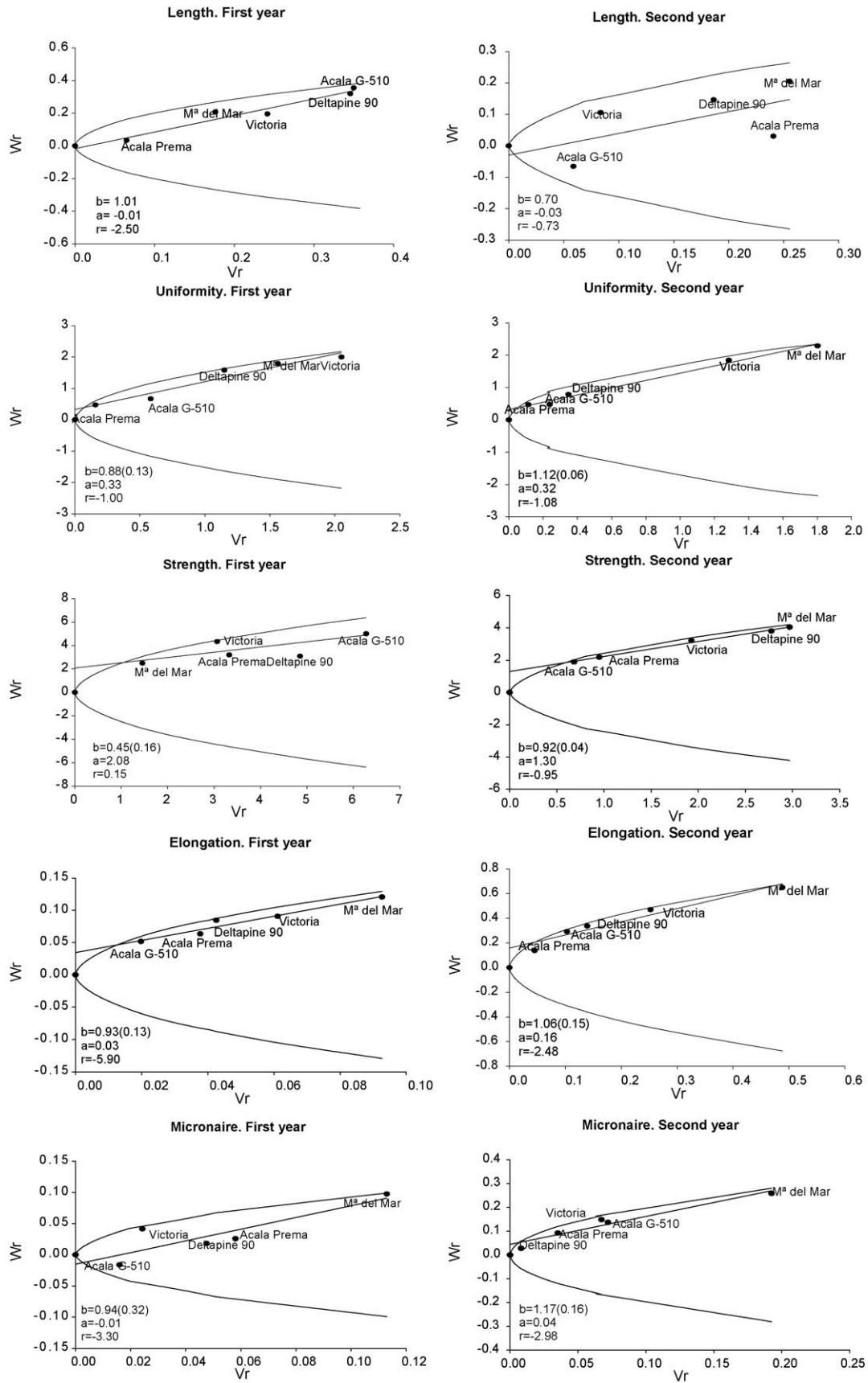


Fig. 2. W_r/V_r plots for the five traits on a half diallel F_1 generation. Analysis of (V_r and W_r) linear regressions (b), intercept of regression line (a) with W_r axis and correlation coefficient between $W_r + V_r$ and mid-parent (r) in both years.

Table 3
Test of diallel assumptions.

Year		Length	Uniformity	Strength	Elongation	Micronaire
First	Test of <i>t</i> for uniform of (Wr – Vr)	0.32	0.65	2.16	0.30	0.28
	Coefficient of regression <i>b</i> (±SE)	1.01 (0.15)	0.88 (0.13)	0.45 (0.16)	0.93 (0.12)	0.93 (0.31)
	Test of <i>t</i> for <i>b</i> = 0	6.80*	6.84*	2.70NS	7.42*	2.95*
	Test of <i>t</i> for <i>b</i> = 1	–0.09NS	0.90NS	3.32*	0.50NS	0.19NS
Second	Test of <i>t</i> for uniform of (Wr – Vr)	0.34	2.10	1.59	0.67	1.40
	Coefficient of regression <i>b</i> (±SE)	0.69 (0.54)	1.12 (0.06)	0.92 (0.04)	1.06 (0.15)	1.17 (0.16)
	Test of <i>t</i> for <i>b</i> = 0	1.26NS	17.23*	21.40*	6.89*	7.31*
	Test of <i>t</i> for <i>b</i> = 1	0.56NS	–1.88NS	1.72NS	–0.42NS	–1.07NS

NS, non-significant; *t*, non-significant in test of *t* for uniformity (Wr – Vr); *t* for *b* = 0, significantly different than zero; and *t* for *b* = 1, not significantly different than one then hypothesis is valid.

* *P* < 0.05.

Table 4
Estimates of genetic components of variation with their standard errors and various ratios between the components.

Years	Parameters	Length (±SE)	Uniformity (±SE)	Strength (±SE)	Elongation (±SE)	Micronaire (±SE)
First	<i>D</i>	0.36* (0.02)	2.17* (0.14)	6.03* (0.88)	0.17* (0.004)	0.07* (0.01)
	<i>F</i>	–0.13NS (0.06)	–0.75NS (0.36)	–2.72NS (2.21)	0.02* (0.01)	0.02NS (0.04)
	H1	0.33* (0.06)	1.13* (0.39)	5.34* (2.38)	0.04* (0.01)	0.11* (0.04)
	H2	0.31* (0.05)	1.01* (0.36)	4.00NS (2.16)	0.03* (0.01)	0.10* (0.04)
	(H1/ <i>D</i>) ^{0.5}	0.96	0.72	0.94	0.48	1.29
	<i>H</i> ²	0.87	0.92	0.93	0.94	0.77
	<i>h</i> ²	0.67	0.79	0.77	0.84	0.43
	Second	<i>D</i>	0.22* (0.06)	2.98* (0.09)	5.79* (0.08)	0.92* (0.03)
<i>F</i>		0.14NS (0.17)	1.32* (0.24)	–0.38NS (0.21)	0.35* (0.09)	0.27* (0.04)
H1		0.45* (0.18)	1.20* (0.26)	0.89* (0.22)	0.23* (0.10)	0.14* (0.04)
H2		0.37* (0.16)	0.97* (0.23)	0.75* (0.20)	0.16NS (0.09)	0.09* (0.04)
(H1/ <i>D</i>) ^{0.5}		1.43	0.63	0.39	0.49	0.60
<i>H</i> ²		0.76	0.94	0.95	0.98	0.89
<i>h</i> ²		0.35	0.75	0.90	0.86	0.70

NS, non-significant; If value of parameter/standard error is >1.96, then the value is significant.

* *P* < 0.05.

was greater than the dominance components in both years (Table 4). The average degree of dominance at each locus ((H1/*D*)^{1/2}) was below 1 in the first year and 0.39 in the second year, denoting partial dominance for this trait. Strength showed high values of *H*² and *h*² in both years (Table 4). The regression line intercept Wr axis (*a*) was over 0 in both years, confirming partial dominance from this trait (Fig. 2). The positive value for the correlation (*r*) between (Wr + Vr) and mid-parent (*y*) in the first year indicated that the recessive genes incremented this trait (Fig. 2). A negative correlation in the second year indicated that the dominant genes were responsible for the increase in strength (Fig. 2).

Table 4 shows that additive (*D*) and dominance components (H1 in both years and H2 the second year) were significant for elongation. The additive effect was greater than the dominance component in both years. The significant and positive value of *F* for elongation in both years indicated an excess of dominant alleles with dominant effects in the parents. The genetic parameter ((H1/*D*)^{1/2}) value below 1, indicated partial dominance for this trait. Elongation showed high values of *H*² and *h*² in both years (Table 4). The regression line intercept Wr axis over the origin (*a*) in both years confirmed the tendency to partial dominance (Fig. 2). Negative correlation (*r*) in both years indicated that the dominant genes were responsible for the variation these traits (Fig. 2).

Results for micronaire showed that dominance effects (H1 and H2) were significant and greater than the significant additive (*D*) component in the first year. Both components were significant in second year, but *D* value was higher than H1 and H2 (Table 4). The significant and positive value of *F* for micronaire in the second year showed an excess of dominant alleles with dominant effects in the parents. Average dominance ((H1/*D*)^{1/2}) was greater than 1 the first year and below 1 the second year. High values of *H*² in both years and *h*² the second year are displayed in Table 4. The *h*² in the

first year was 0.43. The measurement of the average level of dominance provided by the point where the regression line cuts the Wr axis (*a*) presented a negative value the first year, revealing overdominance. However, this value was positive in the second year, indicating partial dominance (Fig. 2). Negative correlation (*r*) in both years indicated that the dominant genes were responsible for this traits variation (Fig. 2).

The variance and covariance (Wr/Vr) plots were examined for all fiber traits (Fig. 2). The cultivar 'Ma del Mar' contained a large proportion of recessive genes for all the traits studied in both years. 'Victoria' contained mostly recessive genes for uniformity in both years, but recessive and dominant genes were found for the other traits. The three cultivars of American origin were grouped together for uniformity, elongation, and micronaire in both years. 'Deltapine Acala 90' displayed a large proportion of recessive genes for length and strength in both years. 'Acala Prema' was an intermediate parent for strength and 'Acala Germain 510' contained mostly dominant genes for this trait in both years.

4. Discussion

Genotype differences for all traits were significant. Interaction [site × genotype] was significant for uniformity, strength, and elongation, suggesting that these traits are related to environmental conditions, in agreement with the results reported by Meredith (1984) without *Verticillium* pressure. Green and Culp (1990), suggested that environmental variability (primarily weather) could influence full realization of the fiber-quality potential of a cotton genotype, in reference to fiber strength and micronaire, without *Verticillium* pressure. Tang (1992), reported that interaction [site × genotype] was significant for both length and strength among 20 parents. However, this interaction was significant only

for strength among 64 F₂ hybrids, under non-*Verticillium* conditions. Bradow and Davidonis (2000) reported that fiber-shape properties, especially length and diameter, depend largely on genetics; furthermore, fiber-maturity properties, which are dependent on deposition of photosynthate in the fiber-cell wall, are more sensitive to changes in the growth environment. The effects of the growth environment on the genetic potential of a genotype modulate both shape and maturity properties to varying degrees. In our study, interaction [site × genotype] was not significant for length or micronaire. By contrast, Ulloa (2006) reported a significant interaction genotype by site for micronaire in the F_{2:3} and F_{2:6} generation without *Verticillium* pressure. Green and Culp (1990) and Sasser and Shane (1996), reported that strong interaction between combined environmental factors and fiber strength suggests that environmental variability can prevent full realization of the fiber-quality potential of a cotton genotype.

Previous studies showed that 'Acala Prema' was the most productive and resistant cultivar while 'Acala Germain 510' and 'Deltapine Acala 90' presented high tolerance to VW (Melero-Vara et al., 1995; Bassett and Kerby, 1996; Oakley, 1998; Boleck et al., 2000; Aguado et al., 2008). Bassett and Kerby (1996) studied the levels of VW resistance in various cotton cultivars, concluding that 'Acala Prema' and 'Acala Germain 510' were the most tolerant cultivars. 'Acala Prema' stood out as the cultivar with the highest values in the most fiber traits studied except for micronaire, for which 'Acala Germain-510' registered the highest value.

Under *Verticillium* conditions, elongation showed a positive and significant correlation with uniformity, strength, and micronaire. Without *Verticillium* pressure, elongation and micronaire were negative and weakly correlated (Ulloa, 2006). With or without *Verticillium* pressure, the relationship between length and strength was positive and significant (Ulloa, 2006). Ulloa (2006), reported that length showed a negative and significant correlation with micronaire, without *Verticillium* pressure, according to our results at site D, where the soil showed the less infestation by *V. dahliae* propagules.

Path-coefficient analysis showed that elongation was possibly the most influential character over seed-cotton yield. In agreement with the findings of Coyle and Smith (1997) and Bradow and Davidonis (2000), strength showed a direct negative effect on seed-cotton yield. Coyle and Smith (1997), suggested that this linkage must be broken before acceptable improvements in fiber strength can be made through genetics, either by classical breeding or at the molecular level. Bradow and Davidonis (2000), reported that the production of stronger fiber appeared to cost the plant both in fiber weight and fiber numbers. Other previous studies, conducted under non-*Verticillium* conditions, also reported negative effects of strength on yield, suggesting that breeding for high fiber strength would sacrifice the primary trait, lint yield (Meredith et al., 1991; May and Taylor, 1998).

Micronaire was the fiber trait most affected by VW (Friebertshauer and DeVay, 1982; Johnson and Goodell, 1998; Bassett and Kerby, 1996). In the present study, VW had the strongest direct effects on strength and micronaire. Length and uniformity did not correlate with symptoms of *Verticillium* wilt; furthermore, both traits registered highly positive correlations under *Verticillium* conditions. This could be because length was completed before the symptoms appeared, but the pathogen could have influenced this trait while colonizing the vascular system of the plant (earlier season) without manifesting external symptoms. According to Hake et al. (1996), boll load, such as that caused by insects, heat, or disease, could tend to increase length and strength. This reasoning could explain why susceptible cultivars ('Ma del Mar' and 'Victoria') showed similar values of length compared to more resistant cultivars ('Acala Germain 510' and 'Deltapine Acala 90').

In general, most of the traits studied presented high values both broad- and narrow-sense heritability, except fiber length the second year. Tang et al. (1996) reported relatively high heritability to fiber length and strength under non-*Verticillium* conditions in F₂ population. In our study, micronaire and uniformity have moderately high-to-high narrow-sense heritability, and additive genetic variance (*D*) was an important source of variation. Contrary to these results, the presence of epistatic gene action in both micronaire and uniformity index was found by Tawhid and Myers (1999) without *Verticillium* pressure. In our work, the dominance effects were greater than the additive component to length, confirming complete dominance, and as overdominance as partial dominance to micronaire. However, Meredith and Bridge (1972) reported little non-additive gene action in fiber length, strength, and fineness in upland cotton without *Verticillium* conditions.

Elongation was the character with the highest positive correlation with seed-cotton yield and showed high values of narrow-sense heritability, suggesting that this trait could be readily modified by selection. However, previous research without *Verticillium* pressure (Meredith, 1984), presented positive correlation among lint yield, fiber elongation, and micronaire, and negative correlation with fiber length and strength. Furthermore, in our study, additive genetic variance (*D*) was the most important source of variation for elongation, indicating easy potential fixation in breeding programs. Elongation fulfills all the assumptions for Hayman analysis and showed higher additive than dominant variance, and high broad- and narrow-sense heritability. These results suggest that elongation could be useful for improving seed-cotton yield and quality fiber, because this trait showed a high and positive correlation with most of the other traits, under *Verticillium* conditions.

In view of both the *W_r/V_r* graphs and the genetic parameters, the genetic system controlling the traits studied showed: total dominance with a tendency towards overdominance for length; partial dominance for uniformity, strength, and elongation; and partial dominance with a tendency toward total dominance for micronaire. For all the traits studied, the degree of dominance at each locus ($(H1/D)^{1/2}$) also indicated low level of dominance except for length, which presented overdominance. In general, these results were similar to those reported under non-*Verticillium* conditions by Jagtap and Kolhe (1986), Luckett (1989) and Ulloa (2006).

The distribution of the array points along the regression line had the following groupings: 'Acala Prema' and 'Acala Germain-510', American origin parents, placed in the dominant zone for most of the studied traits. The other American origin parent, 'Deltapine Acala 90', is placed in the dominant zone only for elongation and micronaire. The parent of Spanish origin 'Ma del Mar' was placed in the recessive zone for the studied traits. 'Acala Prema', 'Acala Germain-510' and 'Deltapine Acala 90' showed a combination of wilt resistance and other useful agronomic characters such as high yield and fiber quality (Aguado et al., 2008).

5. Conclusions

Previous studies under *Verticillium* conditions point to cotton-fiber strength as the trait that integrates the effects of fiber length, uniformity, and micronaire. However, under *Verticillium* conditions, we conclude that elongation is the trait that integrates the most fiber traits studied. Therefore, we suggest that this trait could be useful for improving seed cotton yield and quality fiber, under *Verticillium* conditions.

Until now, micronaire has been the trait most affected by VW. In this work, besides micronaire, strength is very influenced by VW, as shown by the influence of VWI on these traits.

The pure-line breeding may be effective for improving most of the traits ($h^2 > 0.6$) except for fiber length in those cultivars, particularly regarding to elongation. Under *Verticillium* condition,

length showed high non-additive gene action. Length presented lower heritability and significant dominant variance could be indirectly selected by uniformity at the beginning of the breeding program, given that uniformity showed significant and positive correlation at all sites with this trait. Length may be selected directly, in later generations, with more experimental blocks and plots.

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