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BREEDING AND GENETICS

Heritability of Tolerance to Early Foliar Decline in Three Pima Cotton Populations

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INTERPRETIVE SUMMARY

Early foliar decline is a recurring problem of Pima cotton in the San Joaquin Valley of California, where it has been implicated in yield and fiber-quality losses. The disorder is characterized by leaf bronzing, followed by early senescence and premature defoliation. In severe instances, foliar symptoms are accompanied by wilting and death of the main stem apex. The causal agents of early foliar decline are unknown, but nutrient deficiencies, air pollution, and an undetermined plant pathogen have been suggested. Many of the symptoms of early foliar decline are shared in common with potassium deficiency and ozone damage. An increased susceptibility among early maturing, determinate cotton cultivars is another factor apparently shared by early foliar decline, potassium deficiency, and ozone pollution. Although the number of commercially available Pima cultivars is limited, anecdotal evidence suggests that genetic variability for tolerance to early foliar decline exists among them. The objectives of this investigation were to determine the heritability of tolerance and susceptibility to early foliar decline in Pima cotton; to investigate the relationship between early foliar decline and early maturity, determinacy, foliar potassium, yield, and fiber quality; and to identify earlier maturing, early foliar decline-tolerant germplasm.

Three populations (96084, 97016, and 96117) were created for the investigation by crossing putatively early foliar decline-tolerant and -susceptible parents. Evaluation for early foliar decline was conducted in the F_2, F_3, and F_4 generations of the three populations over three successive years at Tulare and Buttonwillow, CA. Agronomic traits were evaluated in the F_3 and F_4 generations, and fiber quality was evaluated in the F_4 generation at the above locations. Heritability estimates obtained between F_2 individual plants and F_3 progeny rows were low (h^2 = 0.14 to 0.19) and appeared to preclude efficient selection for early foliar decline tolerance in the F_2 generation. Higher heritability estimates obtained between F_3 and F_4 generations (h^2 = 0.37 to 0.46) suggested that selection may be feasible in unreplicated early generation (F_3) progeny rows. However, the highest heritability estimates occurred among replicated F_4 progeny rows (h^2 = 0.84 to 0.89), indicating that the greatest selection efficiency could be expected in advanced-generation tests planted at multiple locations. Negative correlations were observed between early foliar decline and plant heights across locations and years, and between early foliar decline and nodes above bloom (r = -0.47 to -0.61) under severe early foliar decline conditions. The negative correlations of early foliar decline ratings with final plant heights and nodes above bloom suggest a positive relationship between early foliar decline severity and early plant maturity, and may indicate difficulty in simultaneous selection for early foliar decline tolerance and early crop maturity. Moderate gains were made in identifying early foliar decline-tolerant germplasm lines possessing incremental increases in earliness.

The impact of early foliar decline on lint yield and fiber quality was measured in replicated tests in 2000. Lint yield was negatively correlated with early foliar decline severity in all F_4 populations at Tulare and in two populations at Buttonwillow. However, yield losses that could be directly attributed to the disorder were confounded by differing levels of earliness and determinacy among progeny lines. Multiple regression results indicated that significant yield losses, attributable to early foliar decline, occurred in lines of population 96084 (212 lb acre^{-1}

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per unit of early foliar decline) and lines of population 96117 (132 lb acre^{-1} per unit of early foliar decline) at Tulare, CA. The impact of early foliar decline upon fiber quality appears to have been influenced by the time of its initiation and its ultimate severity. At the Tulare location, where the disorder appeared early and progressed rapidly, micronaire and elongation were negatively correlated with early foliar decline. Little association between early foliar decline and fiber quality was observed at Buttonwillow, where symptoms appeared later and progressed more slowly.

Although early foliar decline in Pima cotton and bronze wilt in upland cotton share many symptoms and proposed causes, the relationship between the two disorders needs to be established.

ABSTRACT

Early foliar decline is a recurring problem of Pima cotton (*Gossypium barbadense* L.) in the San Joaquin Valley of California, where it has been implicated in yield and fiber-quality losses. The primary objectives of our investigation were to determine the heritability of tolerance and susceptibility to early foliar decline and to identify earlier maturing, early foliar decline-tolerant germplasm. Three populations, created by crossing putatively tolerant and susceptible parents, were evaluated for early foliar decline, agronomic traits, and fiber quality in the F_2, F_3, and F_4 generations over three successive years at Tulare and Buttonwillow, CA. Early foliar decline heritability estimates between F_2 individual plants and F_3 progeny rows were low (h^2 = 0.14 to 0.19) and appeared to preclude efficient selection for tolerance in the F_2 generation. Higher F_3:F_4 heritability estimates (h^2 = 0.37 to 0.46) suggested that selection may be feasible in unreplicated early generation (F_3) progeny rows. However, the highest heritability estimates occurred among replicated F_4 progeny rows (h^2 = 0.84 to 0.89), indicating that the greatest selection efficiency could be expected in advanced generation tests planted at multiple locations. Early foliar decline was negatively correlated with final plant heights of F_3 and F_4 progeny at both Tulare and Buttonwillow, and with nodes above bloom (r = -0.47 to -0.61) of F_4 progeny at Tulare. The above negative correlations suggest that early foliar decline severity is positively related to early plant maturity and increased determinacy, and may indicate difficulty in simultaneous selection for tolerance to early foliar decline and early plant maturity.

In 1995, *California Farmer Magazine* reported a problem occurring in Pima cotton grown in the San Joaquin Valley of California (McMullin, 1995). The disorder was characterized by early senescence, bronzed leaves, and premature defoliation. Yields in severely affected fields were reported to be reduced by as much as one bale per acre, on the basis of past field performance. Although the cause of the malady was unknown, smog was featured as the culprit. Since 1995, the condition has recurred in varying degrees every year. Cotton growers and the popular press commonly refer to the condition as *bronzing* or *bronze wilt*, but another name now in common use by the University of California extension personnel is *early foliar decline*.

Several factors have been nominated as causal agents of early foliar decline, including nutrient deficiencies, pollution, and pathogens. Potassium deficiency frequently has been mentioned as a primary suspect. In their K fertility guidelines, Miller et al. (1997) provided a distinctive set of K-deficiency symptoms, many of which also are common to early foliar decline. Miller et al. reported a general bronzing in K-deficient plants that begins at leaf margins and ultimately encompasses the entire leaf. Leaf edges curl upward, premature wilting of young leaves occurs, and defoliation follows. In comparison, a careful observation of early foliar decline in Pima shows that it also causes leaf bronzing, but that bronzing begins in the interveinal laminae. Curling of leaf edges is not prominent. In the early stages of early foliar decline, young leaves remain healthy, and symptoms first appear on mature leaves five to seven nodes below the plant apex. Only as early foliar decline progresses do young leaves show wilting, followed by defoliation and, in severe instances, death of the apical meristem. Stromberg (1960) reported that with typical March or April planting dates in California's San Joaquin Valley, visual K-deficiency symptoms first appear in upland cotton as plants approach cutout in late July or early August. This also is often the case with early foliar decline. Despite the similarities and dissimilarities of K deficiency and early foliar decline, the relationship between the two is unknown.

Air pollution is another commonly cited candidate for the causal agent of early foliar decline. Ozone damage in particular has been demonstrated to cause early plant cutout and premature leaf senescence in the cultivar Pima S-6 (Grantz and McCool, 1992). Grantz and McCool further demonstrated that exposure to increasing levels of ozone led to losses in yield components and fiber quality. In another study, Grantz and Yang (1996) observed reductions in carbohydrate allocation to roots and decreased foliar K in plants exposed to ozone. Many of the effects of ozone damage reported by Grantz and McCool (1992) are also commonly attributed to early foliar decline.

Leaf spot diseases, often found in association with early foliar decline, have a distinctive set of symptoms. Whereas leaf spot diseases are defined by discrete lesions with distinct borders, defined margins, and necrotic centers (Watkins, 1981); the bronzing of early foliar decline expands to cover large areas of a leaf, has poorly defined margins, and leaves wilt in their entirety. When early foliar decline and leaf spot diseases are found in association, leaf spot lesions generally follow the initial symptoms of early foliar decline. Although early foliar decline can cause extensive defoliation in the absence of leaf spot diseases (R.G. Percy, personal observation, 2000), the presence of leaf spot diseases undoubtedly hastens foliar decline.

A common factor observed in ozone damage, in K deficiency, in leaf spot diseases, and in early foliar decline is an apparent increased susceptibility among early maturing, determinate cotton cultivars. Temple (1990) observed that determinate cultivars were more susceptible to ozone damage and ascribed this susceptibility to the coincidence of peak bloom with periods of high O_3 concentration. He also suggested that indeterminate cultivars might have greater flexibility in responding to ozone damage. Tupper and Calhoun (1996) reported higher soil K requirements by earlier maturing cultivars and correspondingly greater yield responses to K applications. Although the number of Pima cultivars available for comparison is limited, anecdotal evidence suggests that increased susceptibility to early foliar decline also may be related to early maturity and determinacy.

The first reports of early foliar decline in Pima cotton coincided with the initial reports of a “new” disorder in upland cotton (*Gossypium hirsutum* L.) in the Mississippi Delta and the southeastern United States. Called *bronze wilt* or *copper top*, this disorder was characterized by bronzing of leaves, noticeable increases in leaf temperatures, collapse of the youngest leaves in the plant apex, reddening of stems, fruit shed, and rapid wilting (Albers and Guthrie, 2001; Gwathmey et al., 2001). The disorder has been associated by various investigators with cultivar pedigree, early plant maturity, damage to secondary root systems, and the presence of a pathogen (Creech, 1999; Bell, 2000; Phipps, 2000). In an investigation of soil fertility, Gwathmey et al. (2001) reported that neither N, P, nor K fertility altered the incidence or severity of bronze wilt symptoms. Although early foliar decline in Pima cotton and bronze wilt in upland cultivars may be the same disorder, this has not been demonstrated.

The objectives of our investigation were to determine the heritability of tolerance and susceptibility to early foliar decline in Pima cotton; investigate the relationship between early foliar decline and early maturity, determinacy, foliar K, yield, and fiber quality; and to identify earlier maturing, tolerant germplasm.

MATERIALS AND METHODS

Three populations, 96084, 97016, and 96117, were developed for this study. Population 96084 was produced by crossing an early maturing, early foliar decline-susceptible line, 91-209, with a full-season, putatively tolerant line, 8810 (Percy and Turcotte, 1998). Population 97016 was produced by crossing a mid-season, susceptible cultivar, Pima S-7 (Turcotte et al., 1992), with the tolerant cultivar UA 4. Population 96117 resulted from the cross of two mid-season, putatively tolerant lines, P76 and P71 (Percy and Turcotte, 1997).

F_2 Evaluation, 1998

F_2 populations of 96084, 97016, and 96117 were grown in four row plots at a clay loam soil site located 11 km north of Buttonwillow, CA, in 1998. Plots were planted on 4 April. Severe rain and cold temperatures occurred during stand establishment and may have compromised the root health of some plants. Final stands were thinned to about one healthy plant per 39 cm. Twenty-five individual plants per row were rated for early foliar decline, for a total of

100 plants per population. An exception was 96117, which had only 88 plants available for rating. Early foliar decline expression among plants at the time of rating ranged from healthy individuals with green foliage to individuals displaying leaf defoliation and apical death. The following rating scale was used:

1 = Sparse bronze flecks on leaves, first appearing 7 to 10 nodes below plant apex. Plant green and healthy in appearance.

2 = Greater intensity of flecking, but no coalescence of flecks. Plant still appears green and healthy.

3 = Leaves beginning to show areas of coalesced bronzing. Leaves and stem apex still green and maintaining turgor.

4 = Leaves extensively covered with coalesced regions of bronzing. Leaf bronzing extends to plant apex. Leaves and stem apex still alive but exhibiting some flaccidity.

5 = Upper leaves dead and desiccated, or defoliated. Terminal apex appears necrotic or dead. Remaining leaves exhibit coalesced regions of bronzing that extend across leaf surfaces.

All plants that received a rating were individually harvested for seed at season's end.

F_3 Evaluation, 1999

One hundred F_3 progeny rows from 96084 and 97016, and 88 progeny rows from 96117 were planted at a clay loam soil site 11 km north of Buttonwillow, CA, and at a silty loam soil site 9 km west of Tulare, CA, in 1999. Progeny were planted at both locations in randomized, nonreplicated, single row plots, blocked by population. Parent lines and check cultivars were included in each range of the population blocks. Plots were 6 m long, separated by 1.5-m alleys. Final stands were thinned to about one plant per 10 cm. Field management at both locations was the standard farm practices of the respective cooperators.

Ratings and measurements taken in 1999 included early foliar decline ratings, productivity ratings, petiole K measurements, and plant height measurements. A relative scale for early foliar decline severity was adopted in 1999. The susceptible check cultivar, Pima S-7, and susceptible parental lines were assigned a rating on the basis of the predominant individual plant rating within the plot. As in 1998, the rating scale ranged from 1 for a completely healthy plot, to 5 for plots in which plants displaying leaf dessication or defoliation and terminal death predominated. All progeny lines were then rated relative to Pima S-7, and the respective population's susceptible parent cultivar. Ratings were made on two dates (14 September and 1 October) at each location. On both rating dates, all plots were rated by two observers and the two scores were averaged for data analyses. The greatest differentiation among lines occurred on rating dates on which the susceptible check Pima S-7 had progressed to or beyond a grade four, but had not progressed to a uniform grade 5 (terminal death and leaf desiccation). The above rating dates were used in all reported data analyses.

Leaf petiole K levels were measured in replicated parent cultivar plots at the Buttonwillow and Tulare sites on three dates in 1999 that roughly corresponded to early bloom, peak bloom, and post-bloom (7 July, 21 July, and 30 August, respectively). Petioles from the fifth apical node were collected from 25 plants per plot, and were dried, ground, and sent to Dellavalle Laboratory (Fresno, CA) for analyses. At the time of first early foliar decline symptom development (16 September), petiole samples from parent cultivars and 50 randomly selected F_3 lines of populations 96084 and 97016 were collected at the Buttonwillow and Tulare sites and were processed in the above manner.

Due to the late occurrence of early foliar decline in 1999, yield and fiber-quality measurements were not taken, but a visual productivity grade was assigned to individual plots. Plots were assigned a grade from 1 to 10 on a relative scale, with the most productive plots being assigned a rating of 1 and the least productive plots being assigned a rating of 10. Ratings were assigned relative to the Pima S-7 check variety, which was arbitrarily assigned a grade 5.

Selected F_4 Populations, 2000

Twenty F_3 lines from each of the populations 96084, 97016, and 96117 were selected for the production of F_4 lines. Selected lines represented the range of early foliar decline ratings occurring in the F_3 populations, had consistent ratings between the F_2 and F_3 generations, and displayed consistency in F_3 ratings between the two locations. In 2000, the 20 F_4 lines of each population, along with their parents and the susceptible and resistant check cultivars Delta Pine (DP) HTO and Phytogen 57, were planted at a clay loam soil site 8 km northwest of Buttonwillow and at a silty loam soil site 9 km west of Tulare, CA. Plots were arranged in a randomized complete block design with four replicates at each location. Plot size at Buttonwillow was four rows, 15.2 m long, and at Tulare was six rows, 13.4 m long. Final stands were thinned to about one plant per 10 cm. Field management of tests at Buttonwillow and Tulare were the standard practices of the respective cooperators. At the Buttonwillow location, the cooperator grower applied supplemental N and water at the time of first appearance of early foliar decline symptoms, which appeared to ameliorate and delay further symptom development.

Ratings and measurements taken in 2000 included early foliar decline ratings, nodes above open bloom counts, lint yield and yield components, fiber-quality measurements, and plant heights. Early foliar decline ratings were made on three dates (5 September, 13 September, and 22 September) at Buttonwillow and on two dates (7 August and 18 August) at Tulare. Ratings were conducted in the same manner as in 1999, with two individuals taking independent ratings and the two ratings being averaged. The greatest differentiation among lines for early foliar decline occurred on the second rating date at both locations, and these ratings were used in regressions, correlations, and determinations of inheritance. Nodes above open bloom counts were made on all lines immediately after the occurrence of peak bloom in the earlier maturing cultivars Pima S-7 and DP HTO. Five plants from the center two rows of each plot were used. At season's end, a sample of 50 bolls was hand-picked from the center two rows of each plot for fiber analysis and for determination of lint percent, seed size, and boll size. The center two rows of each plot were then machine-harvested for lint-yield determination. A single row height measurement was made in each plot of the replicated tests at the time of harvest, and is referred to hereafter as *plant height*. Fiber samples obtained from the hand-picked boll samples were analyzed using high volume instrumentation (HVI) by Star Lab (Knoxville, TN).

Statistical Analyses

Analyses of variance (ANOVA) were performed on all data collected in 1999 and 2000 using the general linear model procedure of the Statistical Analysis System (SAS Institute Inc., Cary, NC). Due to a lack of replication within test locations in 1999, analyses were performed using locations as replicates. In 2000, F_4 populations were analyzed using a randomized complete block design with four replicates at both locations. Nearest neighbor analysis (Agronomix Software, Winnepeg, MB) was used in analyzing early foliar decline ratings, plant heights, and yield at Tulare in 2000 because of significant field patterns observed at that location. An "east-west" model was employed and analyses of variance were adjusted for east-west trends. Nearest neighbor analysis adjusted plot means for early foliar decline ratings, plant height, and lint yield were used in subsequent correlation and regression analyses.

Heritability estimates of early foliar decline were calculated by parent-offspring regression, using inbreeding coefficients as described by Smith and Kinman (1965). In the instance where unequal generation ranges were encountered, standardized regression coefficients were obtained using the method described by Frey and Horner (1955), and heritability estimates calculated as above. Heritability of early foliar decline within the F_4 generation was calculated using variance components from ANOVA.

RESULTS

Heritability

Significant variation for early foliar decline ratings occurred among progeny lines within populations 96084, 97016, and 96117 in both 1999 and 2000 (Tables 1 and 2). Phenotypic correlations and heritability estimates of early foliar decline between F_2, F_3, and F_4 generations appear in Table 3.

Table 1. *F* values for the variables early foliar decline, final plant height, and plant productivity, obtained from the analyses of variance of F_3 progeny lines within three populations at Tulare and Buttonwillow, CA, in 1999.

Population	No. of progeny	Early foliar decline	Plant height	Productivity
96084	100	1.71**	2.32**	3.54**
97016	88	2.93**	1.51*	1.42**
96117	100	3.42**	4.72**	3.58**

***,**Significant at the 0.05 and 0.01 probability levels, respectively.**

Phenotypic correlations between F_2 individual plants and their F_3 progeny (planted in single plots at two locations) were low (0.33-0.39). Heritability estimates between the F_2 and F_3 generations were correspondingly low and ranged from 0.14 to 0.19. Phenotypic correlations between individual F_3 plots and replicated F_4 plots (both planted at two locations) were much higher than F_2:F_3 correlations and ranged from 0.65 to 0.81. However, F_3:F_4 heritability estimates showed little improvement over F_2:F_3 heritability estimates. The F_4 generation was a subsample of the F_3 generation, and some reduction in heritability between the F_3 and F_4 generations might be expected for this reason. However, directed selection was not practiced during F_3 subsampling other than to ensure that a representative sample was obtained, and therefore selection during subsampling should not have contributed to a reduction in heritability. A biasing factor that did occur between F_3 and F_4 generations was a large reduction in the range of early foliar decline ratings within F_4 populations. This range compression may have been partly due to the averaging across replications that occurred in F_4 populations. When data were standardized in F_3 and F_4 generations by dividing data values by their respective standard deviations, the resulting heritability estimates were much improved. Standardized heritability estimates, based upon standardized regression coefficients, ranged from 0.37 to 0.46. Since the standardized regression coefficients were equivalent to correlation coefficients, the heritability estimates were equivalent to the correlation coefficient divided by the inbreeding coefficient. Heritability estimates based upon variance components in replicated tests of F_4 progeny were quite high, ranging from 0.84 to 0.89. On the basis of these results, low selection efficiency

Table 2. *F* values for the variables early foliar decline, final plant height, nodes above open bloom, and lint yield, obtained from analyses of variance of F_4 progeny lines within three populations at Tulare and Buttonwillow, CA, in 2000.

Location	Population	No. of progeny	Early foliar decline	Plant height	Nodes above open bloom	Lint yield
Tulare	96084†	20	10.56**	3.61**	2.32**	4.71**
	97016	20	12.22**	8.23**	2.27**	4.33**
	96117	20	7.25**	4.11**	2.36**	6.06**
Buttonwillow	96084	20	8.69**	2.56**	1.32	5.22**
	97016	20	4.74**	3.33**	1.67*	1.54
	96117	20	8.31**	5.91**	1.81*	4.46**

***,** Significant at the 0.05 and 0.01 probability levels, respectively.**

† Twenty progeny lines per population were evaluated at each site.

Table 3. Phenotypic correlations and heritability estimates of early foliar decline between F_2, F_3, and F_4 generations.

	F_2, F_3		F_3, F_4			F_4
Population	r	h^2	r	h^2	$h^{2\dagger}$	h^2
		$b/2r_{xy}$		$b/2r_{xy}$	$b'/2r_{xy}$	$\sigma^2_G/(\sigma^2_e/rl+\sigma^2_{GXE}/l+\sigma^2_G)$
96084	0.33**	0.14	0.81**	0.18	0.46	0.89
97016	0.33**	0.17	0.68**	0.17	0.39	0.84
96117	0.39**	0.19	0.65**	0.24	0.37	0.88

***,** Significant at the 0.05 and 0.01 probability levels, respectively.**

† F_3 and F_4 data were standardized by dividing data values by their respective standard deviations, producing a standardized regression coefficient, b'.

for early foliar decline tolerance could be expected in selecting among individual plants of the F_2 generation. Increased selection efficiency could be expected from progeny row selection at multiple locations, making early generation progeny row selection feasible. The highest heritabilities, and therefore the greatest expected efficiency of identification and selection for early foliar decline tolerance, occurred in advanced-generation replicated testing.

Heritability estimates for early foliar decline did not differ greatly among the three populations, 96084, 97016, and 96117. Population 96117, the product of a cross of two mid-season, putatively tolerant lines, displayed heritability estimates as great as populations resulting from crosses of tolerant and susceptible parents. These results suggest that genetic recombination for tolerance factors occurred within the 96117 cross.

Plant Heights and Nodes Above Open Bloom

Final plant heights, measured at harvest, varied significantly among F_3 and F_4 lines within populations 96084, 97016, and 96117 in 1999 and 2000 (Tables 1 and 2). Correlations between F_3 plant heights and early foliar decline ratings were negative in all populations, and ranged from -0.30 to -0.59 at Tulare and from -0.29 to -0.51 at Buttonwillow (Table 4). In 2000, correlations between final plant heights and early foliar decline ratings were somewhat higher at the Tulare location, ranging from -0.60 to -0.73. At the less severely early foliar decline-affected Buttonwillow site, correlations between plant height and early foliar decline rating were significant only in populations 96084 and 96117 (r = -0.71 and -0.60, respectively). Numbers of nodes above open bloom varied significantly among F_4 lines within populations 96084, 97016, and 96117 at Tulare, and among F_4 lines within populations 97016 and 96117 at Buttonwillow in 2000 (Table 2). Nodes above open bloom numbers were negatively correlated with early foliar decline ratings in all populations (r = -0.47 to -0.84) at Tulare (Table 4). No correlation between nodes above open bloom numbers and early foliar decline severity was observed at the less severely affected Buttonwillow site. The lack of correlation between nodes above open bloom and subsequent early foliar decline development at Buttonwillow may have been influenced by supplemental N and water applied by the cooperator at the time of the first signs of plant cutout and the appearance of early foliar decline symptoms. Assuming that nodes above open bloom and final plant height are useful indicators of early maturity and plant determinacy, the above correlations suggest a significant relationship of early maturity and plant determinacy with increased early foliar decline severity. The two estimators of earliness and determinacy, nodes above open bloom and plant height, were highly correlated to each other in populations 96084 and 96117 at the Tulare site (r = 0.72 and 0.75, respectively), but less so at the Buttonwillow location (r = 0.42 and 0.51, respectively).

Table 4. Correlation of early foliar decline (EFD) ratings with plant heights, nodes above bloom, productivity ratings, and lint yield in F_3 and F_4 progeny lines at Tulare and Buttonwillow, CA, in 1999 and 2000.

		Correlations with F_3 EFD ratings		Correlations with F_4 EFD ratings †		
Location	**Population**	**Plant height**	**Productivity rating**	**Plant height†**	**Nodes above bloom**	**Lint yield†**
		r	*r*	*r*	*r*	*r*
Tulare	**96084**	**-0.47****	**0.18**	**-0.73****	**-0.61****	**-0.82****
	97016	**-0.59****	**0.25***	**-0.69****	**-0.84****	**-0.75****
	96117	**-0.30****	**0.46****	**-0.60****	**-0.47***	**-0.60****
Buttonwillow	**96084**	**-0.40****	**0.18**	**-0.71****	**-0.39**	**-0.63****
	97016	**-0.29****	**0.27****	**-0.60****	**-0.14**	**-0.46***
	96117	**-0.51****	**0.41****	**-0.25**	**-0.16**	**-0.17**

***,** Significant at the 0.05 and 0.01 probability levels, respectively.**

† Data used in correlations at Tulare were adjusted using nearest neighbor analysis.

Foliar Potassium

Potassium levels in petioles were measured in replicated parent cultivar plots at the Buttonwillow and Tulare sites on three dates in 1999 that roughly corresponded to early bloom, peak bloom, and post-bloom (7 July, 21 July, and 30 August, respectively). In cross 97016, the putatively tolerant parent, UA 4, displayed higher K levels than the susceptible Pima S-7 parent on all dates (Table 5). The putatively tolerant parent of cross 96084, 8810, displayed higher K levels than the susceptible line 91-209 on the latter two dates. No differences in K were noted between the two putatively tolerant parents of cross 96117 (P71 and P76) at early bloom, peak bloom, or post-bloom. Petiole K levels of all parents were adequate for the growth stage of the plant at early and peak bloom, according to ranges determined by the University of California (Miller et al., 1997). Petiole K measurements taken at the two locations at the time of first symptom development (16 September) revealed K differences between parent cultivars of the crosses 96084 and 96117. In 96084, the putatively tolerant parent 8810 exceeded 91-209 in foliar K, and in cross 96117, P71 exceeded P76.

Foliar K levels also were measured in 50 randomly selected F_3 lines of populations 96084 and 97016 at the time of first symptom development. Differences in K among the lines approached significance at the 5% level (P = 0.057). Petiole K ranged from 0.4 to 1.5% across F_3 lines at the Buttonwillow site, and from 0.2 to 1.3% across lines at the Tulare site. Negative correlations were obtained between petiole K levels and early foliar decline severity at both the Buttonwillow (-0.44) and Tulare (-0.53) sites. Across both locations, the correlation between petiole K levels and early foliar decline expression was -0.56. Foliar K levels of the 50 progeny lines at the time of first symptom development displayed a low, but positive relationship with final plant heights at both Buttonwillow and Tulare (r = 0.45 and 0.42, respectively), suggesting a relationship between indeterminate growth habit and higher K levels.

Table 5. Leaf petiole K concentrations of parent cultivars on four dates in 1999.

		Percent K†			
Cross	**Parent**	**7 July**	**21 July**	**30 Aug.**	**16 Sept.**
96084	8810	3.9	3.4a	1.0a	0.7a
	91-209	3.6	2.9b	0.8b	0.5
97016	UA 4	4.5a	4.1a	1.7a	1.0
	Pima S-7	3.8b	3.5b	1.4b	0.9
96117	P76	3.7	3.2	1.3	0.7b
	P71	3.8	3.3	1.4	0.9a

† Within columns, means of parental pairs followed by different letters are significantly different according to LSD (0.05).

Yield

Yield harvests were not performed on F_3 populations in 1999 because of the late onset of early foliar decline and its apparent lack of effect upon yield. Progeny rows were rated for productivity at season's end, and analyses of ratings (using locations as replication) revealed differences among progeny within the three populations (Table 1). High ratings (i.e., low productivity) showed a weak correlation with increased early foliar decline severity in populations 97016 and 96117 at both the Buttonwillow and Tulare locations (Table 4). Due to the late onset of symptoms, it is thought that these positive correlations between lower productivity and increased early foliar decline severity did not reflect yield losses directly attributable to early foliar decline. The positive association between lower productivity and early foliar decline severity was more likely the indirect result of the positive association of early foliar decline severity with increasing earliness and determinacy (estimated by nodes above bloom and plant heights). Increased earliness and determinacy of cultivars are yield-limiting factors independent of the presence of early foliar decline.

Lint yield at the Buttonwillow site greatly exceeded the yield of the Tulare location in 2000 (1192 kg ha^{-1} vs. 695 kg ha^{-1}). At Buttonwillow, yield differences among F_4 progeny occurred in populations 96084 and 96117 (Table 2). At the more severely early foliar decline-affected Tulare site, yield differences among F_4 lines were confined to 96117 (data not shown). However, strong field patterns for early foliar decline were noted at Tulare, suggesting that the use of nearest neighbor analysis was appropriate. Using nearest neighbor analysis, yield differences among F_4 progeny were observed in all three populations (Table 2). Yield was negatively correlated with early foliar decline severity in all

Table 6. *t* values of parameter estimates from the multiple regression of early foliar decline ratings, nodes above bloom, and final plant height upon lint yield in populations grown at Buttonwillow and Tulare, CA, in 2000.

		Populations		
Location	**Variable**	**96084**	**97016**	**96117**
Buttonwillow	**Intercept**	**1.45**	**3.37****	**0.49**
	rating	**-1.78**	**0.91**	**-1.17**
	Nodes above bloom	**0.21**	**0.38**	**2.04**
	Plant height	**0.88**	**0.47**	**0.90**
Tulare	**Intercept**	**2.92****	**1.34**	**1.44**
	EFD rating	**-4.13****	**-1.48**	**-2.26***
	Nodes above bloom	**-0.95**	**-1.16**	**-1.13**
	Plant height	**0.75**	**4.30****	**3.12****

***,** Significant at the 0.05 and 0.01 probability levels, respectively.**

populations at Tulare and in two populations at Buttonwillow (Table 4). These correlations were higher at the more severely early foliar decline-affected Tulare site than at Buttonwillow, and ranged from -0.60 to -0.82. Yield losses directly attributable to early foliar decline could not be determined by simple correlation, however, because of the confounding effects of cultivar earliness and determinacy. Nodes above bloom and plant heights, both estimators of earliness and determinacy, correlated positively with yield (data not shown) and negatively with early foliar decline. Therefore, shorter, more determinate lines had lower yield potentials, independent of any yield losses due to increased early foliar decline susceptibility. Multiple regressions, run to determine the effect of early foliar decline upon yield (adjusted for the effects of nodes above bloom and plant height), produced significant partial regression coefficients in only two populations at the Tulare location (Table 6). In population 96084, a yield decrease of 237 kg ha^{-1} was observed for every unit increase in early foliar decline severity (Fig. 1). A yield decrease of 148 kg ha^{-1} per unit increase in early foliar decline was observed in 96117.

Fiber

F_4 progeny of populations 96084, 97016, and 96117 differed in fiber length, strength, elongation, and micronaire at both Tulare and Buttonwillow in 2000 (data not shown). At the Tulare location, which was more severely affected by early foliar decline, early foliar decline ratings were negatively correlated with micronaire in all three populations (Table 7). In two populations, 96084 and 96117, early foliar decline ratings were negatively correlated with elongation, and in one population, 96084, early foliar decline ratings were negatively correlated with fiber strength. At the Buttonwillow location, which was less severely affected by early foliar decline, no associations between early foliar decline ratings and micronaire were observed. Fiber strength and elongation were negatively related to early foliar

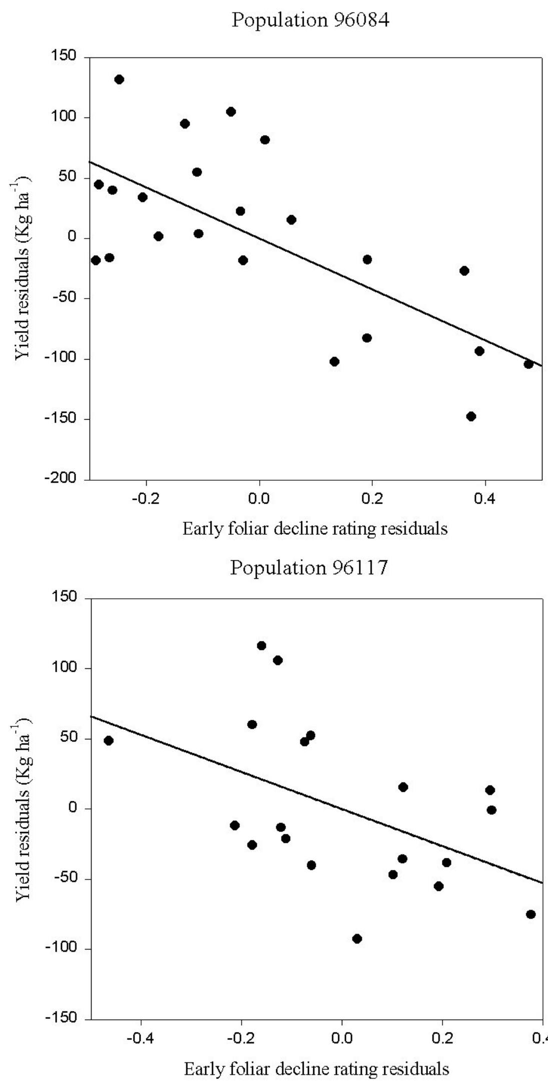

Fig. 1. Relationship between early foliar decline severity and fiber yield in populations: (a) 96084 and (b) 96117 at Tulare, CA, in 2000. Data points represent early foliar decline and yield residuals in a partial regression plot derived from the multiple regression of early foliar decline ratings, nodes above bloom measurements, and plant heights against yield.

Table 7. Correlation of early foliar decline (EFD) ratings with the fiber traits length, strength, elongation, and micronaire (measured on HVI instrumentation) in F_4 progeny lines at Tulare and Buttonwillow, CA, in 2000.

		Correlations with F_4 EFD ratings			
Location	Population	Length (2.5% SL)	Strength (T1)	Elongation (E1 %)	Micronaire
		r	*r*	*r*	*r*
Tulare	**96084**	**0.04**	**-0.46***	**-0.55****	**-0.76****
	97016	**0.30**	**-0.05**	**-0.44***	**-0.80****
	96117	**0.34**	**-0.06**	**-0.20**	**-0.59****
Buttonwillow	**96084**	**0.37**	**-0.47***	**-0.49***	**-0.39**
	97016	**0.37**	**-0.08**	**-0.41**	**-0.43**
	96117	**0.09**	**-0.02**	**-0.34**	**-0.27**

***,** Significant at the 0.05 and 0.01 probability levels, respectively.**

decline severity in one population, 96084. No relationship was found between early foliar decline ratings and fiber length at either location.

DISCUSSION

Low heritability estimates between F_2:F_3 generations preclude efficient selection for early foliar decline tolerance in individual F_2 plants. Higher heritability estimates between F_3:F_4 generations suggest that selection may be feasible in unreplicated early generation progeny rows, planted at multiple locations. The greatest selection efficiencies, however, will occur in replicated advanced generation tests, as indicated by the high heritability estimates among replicated F_4 progeny rows. The high heritability estimates occurring in replicated advanced-generation tests indicate that tolerance to early foliar decline is a highly identifiable and heritable trait under these conditions. With adequate replication, early generation testing of F_2 populations may be a viable tool in identification of populations possessing tolerance. The negative relationship of early foliar decline severity with nodes above bloom and plant height indicates potential difficulties in attempting simultaneous selection for early foliar decline tolerance and early maturity.

Although petiole K levels differed among tolerant and susceptible parent lines at early and peak bloom, the levels of K observed in all parents were considered to be “adequate” (Miller et al., 1997). Negative correlations between petiole K levels and early foliar decline did occur at the time of symptom development. However, because of the preexistence of early foliar decline symptoms, it is not possible to determine from the available data whether foliar-K deficiencies are a cause of early foliar decline or an effect of the disorder. Negative correlations occurred between lint yield and early foliar decline severity in all populations at Tulare and in two populations at Buttonwillow. However, yield levels may have been affected by differences in earliness and determinacy among progeny lines, as well as losses due to early foliar decline. Multiple regression results that indicated significant yield reductions that can be directly attributed to early foliar decline occurred in two populations at the Tulare site in 2000. The impact of early foliar decline upon fiber quality appears to have been influenced by the time of early foliar decline initiation and its ultimate severity. At the Tulare location, where the disorder appeared early and progressed rapidly, micronaire and elongation were negatively correlated with early foliar decline. Little association between early foliar decline and fiber quality was observed at Buttonwillow, where symptoms of the disorder appeared later and progressed more slowly.

Only moderate gains were made in identifying early foliar decline-tolerant germplasm lines possessing incremental increases in earliness. The authors suggest that earlier maturity and increased determinacy may be contributing factors to early foliar decline. When flowering commences in cotton, there is a major change in allocation of photosynthates and nutrients from vegetative growth to the development of fruiting structures. With high harvest indices and compressed fruiting periods, early maturing cultivars may be placing stresses on their root systems at this time. Roots may respond by becoming inefficient suppliers of necessary nutrients to foliar portions of the plant. Leaves, in turn, may then express nutrient-deficient symptoms and become more susceptible to environmental stresses such as ozone. Any biotic or abiotic factors that damage or compromise root systems before fruiting would probably only increase and exacerbate expression of early foliar decline. Further research such as defruiting experiments performed on early maturing cultivars or deliberate damaging of root systems of full-season cultivars might produce information relevant to the above hypothesis.

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