

BREEDING & GENETICS

QTL Analysis of Stomatal Conductance and Relationship to Lint Yield in an Interspecific Cotton

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INTERPRETIVE SUMMARY

Cotton is routinely grown in the hot, irrigated areas of the U.S. Southwest. Extended periods of extremely high temperatures are common in these areas during the critical stage of peak flowering. In pima cotton, and to a certain extent upland cotton, lint yields can be reduced by this heat stress.

Cotton plants have a built-in mechanism to cool themselves by movement of water from the stomata in the leaves, which provides a form of evaporative cooling. The ability of plants to do this is called stomatal conductance. Plants with high stomatal conductance move more water from their leaves than do plants with low values, and, therefore, protect critical physiological processes in the leaf.

Typically, pima cotton has lower values of stomatal conductance than do adapted upland cultivars in irrigated environments; so, pima cotton is more susceptible to severe heat stress. Researchers in these western growing regions have studied the physiological and genetic parameters of stomatal conductance. The recent development of interspecific (pima × upland) genetic populations and new DNA mapping technologies provide powerful tools for dissection of this physiological trait.

This research was conducted on an interspecific genetic population that was segregating for genes from upland and pima cotton. The variation for stomatal conductance was great, providing an

opportunity for selection and application of DNA markers to tag the trait in cotton. Divergent selection was based entirely on stomatal conductance, which resulted in a high group and low group for this physiological trait. The results validated the hypothesis that selection for high stomatal conductance had an indirect effect on lint yield, which was increased significantly. The effect on lint yield appears not to be related to linkage drag (retention of high-yielding upland genes), because the selected lines performed very differently, depending on the environment.

Selection for low stomatal conductance significantly reduced lint yield. In addition, chromosomal regions were identified with DNA markers that controlled this trait. The DNA markers could be used in a cotton breeding program to assist in selection for this difficult-to-measure physiological trait. The end product would be cotton cultivars with high and stable lint yield in a variety of heat-stress irrigated environments.

ABSTRACT

Extended periods of high temperature can reduce cotton (*Gossypium hirsutum* L. and *G. barbadense* L.) lint yield, even under adequate irrigation. High stomatal conductance may confer some adaptive advantage to genotypes that experience supra-optimum temperatures. The primary objective of this research was to practice divergent selection for stomatal conductance in a segregating population (n = 118 F_{2,3} progenies) derived from the cross NM24016/TM1. Divergent selection for high and low stomatal conductance was practiced in Maricopa, AZ, in 1996. DNA was isolated from all 118 F₂ plants in 1995 and a linkage map produced with 199 random amplified polymorphic (RAPD) and simple sequence repeat (SSR) DNA markers. Genetic analysis of the replicated F₃ families in 1996 at Maricopa

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Abbreviations: QTL, quantitative trait loci; RAPD, random amplified polymorphic DNA; SSR, simple sequence repeat.

permitted identification of quantitative trait loci (QTL) influencing stomatal conductance. Replicated experiments of 20 selected $F_{2,4}$ progeny (10 with high, 10 with low stomatal conductance) were grown in Maricopa and Las Cruces in 1997. The 10 families selected for high stomatal conductance in 1996 averaged $542.6 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ at Maricopa in 1997 and were significantly ($P = 0.0001$) different from the mean of the low families ($472 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$). The two selected groups were not significantly different for stomatal conductance at Las Cruces ($P = 0.0631$). Lint yield was significantly ($P = 0.0027$) affected by selection for stomatal conductance in Maricopa. The $F_{3,4}$ family group with high stomatal conductance produced the highest cotton lint yield averaging 1842 g plot^{-1} while the family with low stomatal conductance averaged 1655 g plot^{-1} . Two putative QTLs for stomatal conductance were identified on two cotton linkage groups.

Lint yield of cotton can be dramatically reduced by supra-optimal temperatures during peak reproductive development in irrigated conditions in the U.S. Southwest. Recent studies with pima have shown that increases in stomatal conductance have accompanied increases in cotton lint yields (Lu et al., 1994, 1998; Lu and Zeiger, 1994). The level of stomatal conductance at high temperature was positively correlated with stomatal sensitivity to temperature and independent of photosynthesis (Lu et al., 1996).

Our working hypothesis was that selection for high yields has imposed indirect selection pressure for elevated stomatal conductance at supra-optimal temperature under irrigated environments. This increased conductance may reduce leaf temperatures and confer tolerance to high temperatures, especially during critical fruiting periods.

Genetic modifications of the sensory transduction pathway(s) are required in guard cells for genetically stable changes in stomatal conductance (Zeiger, 1983). This higher level of conductance provides an avoidance mechanism for heat tolerance in hot environments that would not prevail or contribute to higher lint yields under cooler environments, such as the San Joaquin Valley in California (Lu et al., 1998). The adaptive

advantage of greater stomatal conductance would be absent at lower leaf temperatures.

Genetic studies of stomatal conductance have been restricted to each cultivated species (upland and pima cotton) and not interspecific hybrid populations. Roark and Quisenberry (1977) found stomatal conductance to be under genetic control in upland cotton. Percy et al. (1996) estimated relatively low heritabilities for the trait in pima populations and reported existence of dominance and epistatic interactions controlling the trait. Divergent selection for stomatal conductance in a pima segregating population revealed that high yielding F_4 progeny were derived predominantly from F_2 plants with high levels of stomatal conductance (Radin et al., 1994).

As a result of selection for high lint yields under hot environments in Arizona, the stomatal conductance of some recent pima cultivars has approached that of upland cotton (Radin, 1992). Genes for high levels of stomatal conductance from upland cotton may have contributed to the increases in the trait in advanced pima lines selected for high lint yields in hot Arizona environments (Lu et al., 1994).

Introgression of genes between upland and pima cotton has been a long-standing goal of cotton breeders. Traits that have been the target of introgression include heat tolerance from upland sources and fiber quality from pima germplasm. The degree of introgression is hindered by genetic breakdown in segregating interspecific breeding populations (Stephens, 1949).

Genetically stable lines that exhibit significant combinations of upland and pima chromatin have been developed (Tatineni et al., 1996; Cantrell and Davis, 1993). These genotypes display a continuous spectrum of morphological traits between the two parental species. The genetic distance of these lines from typical upland TM1 has been determined using molecular and morphological markers. Evaluation of these lines for stomatal conductance under heat-stress conditions reveals that lines more genetically similar to TM1 have higher stomatal conductance values than those more similar to pima 3-79 (Cantrell and Zeiger, 1995, personal communication).

One of these introgressed lines, denoted as NM24016, exhibits significant introgression from

upland and pima (Cantrell et al., 2000). The variability derived from hybridization of NM24016 with upland TM1 would provide a valuable opportunity for associating introgressed chromosome regions with physiological traits, such as stomatal conductance.

Most important characteristics of agricultural crops are quantitatively inherited, and stomatal regulation appears to be one such trait. The location and effects of the genes controlling quantitative traits can be determined by DNA marker-based genetic analysis. A region of the genome linked to or associated with DNA markers that affects a quantitative trait is defined as a quantitative trait locus (QTL) (Geldermann, 1975). Shappley (1996) provided the first linkage map of QTLs in an upland cotton cross. Recently, other cotton QTLs have been identified for fiber quality (Shappley et al., 1998; Jiang et al., 1998). To date, no QTLs have been reported for physiological traits in cotton.

The objectives of this study were: (i) to determine the effect of divergent selection for stomatal conductance on lint yield in a diverse segregating population derived from the cross NM24016/TM1, (ii) to determine the stomatal conductance and lint yield of selected progenies in two environments representing drastically different temperatures during peak fruiting periods, and (iii) to utilize DNA markers and a linkage map to identify QTLs controlling stomatal conductance.

MATERIALS AND METHODS

Genetic Materials

The initial genetic population consisted of 118 F_2 plants derived from the cross NM24016/TM1 made in the greenhouse in 1994. This population was grown in a space-planted nursery in Las Cruces, NM, in 1995. All flowers on each F_2 plant were manually self-pollinated to generate 118 $F_{2,3}$ families. NM24016 is an inbred line with the interspecific pedigree, H12156/2/77-505/Russian 5904. Introgression from both species into this line was deliberate to achieve maximum stabilized expression of combinations of traits from both parental species.

In previous experiments NM24016 has exhibited stomatal conductance values intermediate between

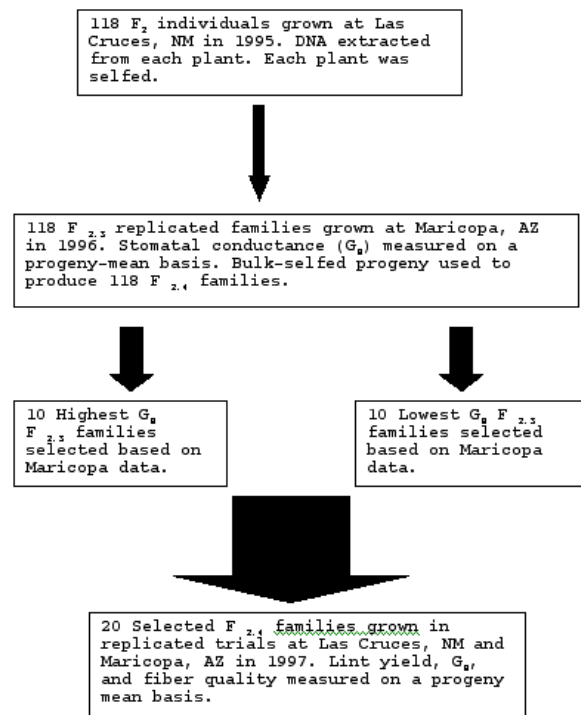


Fig. 1. Flowchart of derivation and evaluation of progeny from the population, NM24016 × TM1 cotton.

upland TM1 and pima 'S-6' (Cantrell, unpublished data, 1995). TM1 is an upland cotton genetic standard and is derived from 'Deltapine 14' (Kohel et al., 1970).

The derivation and evaluation of progeny from NM24016 / TM1 is displayed in Fig. 1. The 118 $F_{2,3}$ families were grown in a replicated experiment at Maricopa, AZ, in 1996. The experiment consisted of two replications of a randomized complete block design with each family represented as a single 8-m plot containing approximately 50 plants. Each $F_{2,3}$ family was also grown as a single 10-m row, comprised of approximately 30 plants, in the genetics nursery at Las Cruces, NM, in 1996. The bulk harvest of each row in the genetics nursery produced ample $F_{2,4}$ seed for testing in 1997.

Stomatal Conductance Measurements and Selection

Stomatal conductance (H_2O) was measured on the youngest fully expanded mainstem leaf of five random plants from each of the 118 $F_{2,3}$ at Maricopa in 1996. Measurements were taken at 1300 to 1500

h with a LI-1600 Steady State Porometer (LI-COR Inc., Lincoln, NE) in late July, which corresponds to peak flowering. Plant measurements were repeated on two consecutive days to produce a sample of 10 measurements per plot. Stomatal conductance ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) on an $F_{2,3}$ plot mean basis was expressed as the mean of these 10 measurements.

Divergent selection was practiced for high and low stomatal conductance in 1996. The highest 10 families and the lowest 10 families were selected for further evaluation in 1997. The selected $F_{2,4}$ families ($n = 20$) were planted at two locations, Las Cruces, NM, and Maricopa, AZ, in 1997. All plots were grown under flood irrigation conditions with agronomic and pest control practices recommended for the respective growing areas.

The soil type at Las Cruces is a Glendale loam (fine-silty, mixed, superactive, calcareous, thermic Typic Torrfluvents, $\text{pH} = 8.0$). Maricopa experiments were grown on a Casa Grande sandy loam (fine-loamy, mixed, superactive, hyperthermic Typic Natrargids). Las Cruces is typical of cooler high-elevation (>1000 m) irrigated cotton production areas where Maricopa is characteristic of low elevation (<200 m) hotter growing environments.

An $F_{2,4}$ family was represented by a single two-row plot that was 10 m in length with 100 seeds planted per row. The experiment at each location was arranged as three replications of a randomized complete block design. Stomatal conductance was recorded on a plot-mean basis in a similar manner to the previous year.

Lint Yield and Statistical Analysis

All replicated field plots in 1997 were machine harvested for yield determination. Random samples of 25 bolls were taken from each two-row plot for lint percent determination. To determine lint yield, seed-cotton was weighed on the 25-boll sample, then ginned to calculate lint percentage. Seed-cotton yield per plot then was transformed to lint yield (g plot^{-1}), using the calculated lint percentage from the sample.

The data from 1997 were subjected to conventional analysis of variance (ANOVA) using PROC MIXED within SAS (Littell et al., 1996). Locations and entries in the analysis were considered fixed effects.

The divergent selection for stomatal conductance in the F_3 generation and subsequent evaluation of high and low groups of F_4 progeny in the next generation permits calculation of realized heritability with the formula (Fehr, 1987):

$$h^2 = \frac{[(\text{Mean high } F_{2,4} - \text{Mean low } F_{2,4}) / (\text{Mean high } F_{2,3} - \text{Mean low } F_{2,3})]}{}$$

DNA Markers and QTL Analysis

In 1995, DNA was isolated from all 118 F_2 plants of the cross NM24016/TM1 according to the method of Paterson et al. (1994). We used 199 DNA markers (RAPDs and SSRs) to construct a genetic linkage map of NM24016/TM1, F_2 . There were 28 linkage groups with a total map distance of 1058 cM. Several of the linkage groups were assigned to cotton chromosomes by use of appropriate aneuploid stocks (R.G. Cantrell, 1999, personal communication).

The QTL analysis of stomatal conductance obtained from the 118 $F_{2,3}$ progeny means in 1996 at Maricopa was performed by two computer programs, QTL Cartographer V.1.12 (Basten et al., 1997) and QGENE V.2.26 (Nelson, 1996). The computer program QTL Cartographer uses simple linear regression, stepwise regression, interval mapping, and composite interval mapping that extends the regression equation to include more markers and uses remaining markers as co-factors in order to remove the effects of multiple QTLs. The linkage groups are scanned to determine whether the likelihood ratio (LR) test statistic is increasing or decreasing. Assume L_1 is the likelihood that the QTL is located in the interval flanked by the markers and L_0 is the likelihood there is no QTL in the interval (i.e., the null hypothesis or H_0). The log-odds ratio (LOD) is defined as:

$$LOD = -\log (L_0/L_1)$$

The likelihood ratio test statistic (LR) calculated by QTL Cartographer according to Basten et al. (1997) is:

$$\begin{aligned} LR &= -2\ln (L_0/L_1) = -2\ln 10^{-LOD} \\ &= 2(\ln 10)LOD = 4.605 LOD \end{aligned}$$

And thus

$$LOD = -\log \exp \{-(LR / 2)\} \\ = (1/2)(\log e)LR = 0.217LR$$

The threshold value of 9.21 for LR was set for detection of a QTL. This corresponds to a LOD score of 2.0. In addition, a QTL was detected when the tail probability of the *F* statistic (from the least squares regression) was significant at the 0.01 probability level assuming one and *n*-1 degrees of freedom in the numerator and denominator, respectively.

QGENE was used to display the effect of individual markers in an interval identified as a QTL by QTL Cartographer.

RESULTS

The *F*₃ generation exhibited extensive variation for stomatal conductance at Maricopa in 1996 (Fig. 2). Stomatal conductance in the *F*_{2,3} families ranged from 486 to 814 mmol m⁻² s⁻¹, indicating transgressive segregation for the trait, because the stomatal conductance for TM1 was 721 mmol m⁻² s⁻¹ and NM24016 was 630 mmol m⁻² s⁻¹. When divergent selection was practiced for stomatal conductance in the *F*₃ generation at Maricopa, the mean of the high set (*n* = 10) was 796 ± 8 mmol m⁻² s⁻¹ and mean of the low set (*n* = 10) was 568 ± 6 mmol m⁻² s⁻¹.

Divergent selection for stomatal conductance in the *F*₃ generation produced dramatic results in the *F*₄ generation.

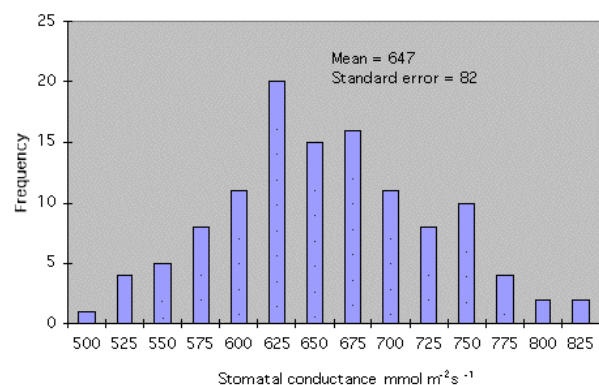


Fig. 2. Distribution of *F*_{2,3} cotton progeny (*n* = 118) for stomatal conductance at Maricopa, AZ, in 1996.

Table 1. Combined analysis of variance for stomatal conductance (*g*_s) and lint yield at Las Cruces, NM and Maricopa, AZ in 1997.

Source	df	Stomatal conductance		Lint yield	
		Mean square	Pr > F	Mean square	Pr > F
Locations	1	130670	0.0001	9130	0.6836
Rep (Locations)	4	13931	0.0057	126752	0.0588
<i>F</i> _{2,4} progeny	18	7358	0.0134	653097	0.0001
High vs. Low <i>g</i> _s progeny	1	78300	0.0001	176164	0.0732
Locations X Progeny	18	11681	0.0736	365218	0.0106
Pooled Error	94	3572	- - -	53709	- - -

Table 2. Means of high and low stomatal conductance (*g*_s, mmol m⁻² s⁻¹) groups of *F*_{2,4} progeny in Maricopa, AZ and Las Cruces, NM in 1997.

Source	Maricopa 1997		Las Cruces 1997	
	Mean	Range	Mean	Range
	mmol m ⁻² s ⁻¹			
High <i>g</i> _s <i>F</i> _{2,4} (<i>n</i> = 10)	542.6a †	402.1–616.1	314.1a †	193.0–535.1
Low <i>g</i> _s <i>F</i> _{2,4} (<i>n</i> = 10)	471.8b	301.0–610.3	282.8a	193.3–452.6
DPL90	546.7	-	386.5	-
Pima S	476.7	-	315.6	-

† Progeny means within a column followed by a different letter are significantly different at the 0.05 probability level.

The mean stomatal conductance of the selected groups differed significantly (*P* = 0.0001) when averaged across environments in 1997 (Table 1). Although the genotype-by-environment interaction for stomatal conductance was not significant (*P* = 0.0736), it is informative to compare the results of the contrasting locations in 1997. The 10 *F*_{2,4} families selected for high stomatal conductance in 1996 averaged 542.6 ± 54 mmol m⁻² s⁻¹ at Maricopa in 1997 and were significantly (*P* = 0.0001) different from the mean of the low families (471.8 ± 74 mmol m⁻² s⁻¹) (Table 2). The two selected groups were not significantly different for stomatal conductance at Las Cruces (*P* = 0.0631).

The differences in stomatal conductance may reflect the higher average daily temperatures at the time of conductance measurement in Maricopa (38 °C) than at Las Cruces (34 °C).

Lint yield was significantly affected by selection for stomatal conductance (Table 1). However, the genotype-by-location interaction for this trait was significant (*P* = 0.0106). The difference between the high and low stomatal conductance groups mirror the results for stomatal conductance as discussed above

Table 3. Means for lint yield (g plot⁻¹) of high and low stomatal conductance (g_s) groups of F_{2,4} progeny in Maricopa, AZ and Las Cruces, NM in 1997.

Source	Maricopa 1997		Las Cruces 1997	
	Mean	Range	Mean	Range
	-----g plot ⁻¹ -----			
High g _s F _{2,4} (n = 10)	1842a †	941-2588	1749a †	1089-2400
Low g _s F _{2,4} (n = 10)	1655b	699-2368	1782a	1168-2734
DPL90	2809	-	2674	-
Pima S-6	2067	-	1793	-

† Progeny means within a column followed by a different letter are significantly different at the $P = 0.05$.

Table 4. Informative DNA markers for stomatal conductance in F_{2,3} families at Maricopa in 1996.

Marker	Parent	P †	R ² ‡	Stomatal conductance mmol m ⁻² s ⁻¹		
				A(+) Aa A(-)		
A13670	TM1 §	0.013	6	653.3	-	618.3
S3	TM1 §	0.004	8	656.3	-	612.5
G3800	Co-dom. ¶	0.016	7	623.1	664.2	637.9

† Probability for the single marker analysis (QGENE).

‡ R² describes the amount of phenotypic variation in stomatal conductance explained by each individual marker (QGENE).

§ Denotes the parent fragment present A(+) for dominant markers.

¶ The TM1 fragment is denoted by A(+) as homozygous, NM24016 is homozygous A(-), and Aa is heterozygous.

(Table 2). The progeny selected for high stomatal conductance were significantly ($P = 0.0027$) higher yielding in Maricopa than those selected for low stomatal conductance. The two groups of selected progeny had similar mean lint yields at Las Cruces in 1997 ($P = 0.5296$) (Table 3).

Realized heritability (0.41) and narrow sense heritability (0.44) estimates of stomatal conductance obtained from these families were moderate, indicating enough genetic variability in this trait to prove valuable for the elucidation of the genetic regulation of stomatal conductance.

QUANTITATIVE TRAIT LOCI (QTL) FOR STOMATAL CONDUCTANCE

The degree of association of a putative QTL for stomatal conductance with molecular markers mapped in the F₂ generation was assessed by simple linear regression, interval mapping, and composite interval mapping in the F₃ generation. Two putative QTL intervals for stomatal conductance (g_s) were

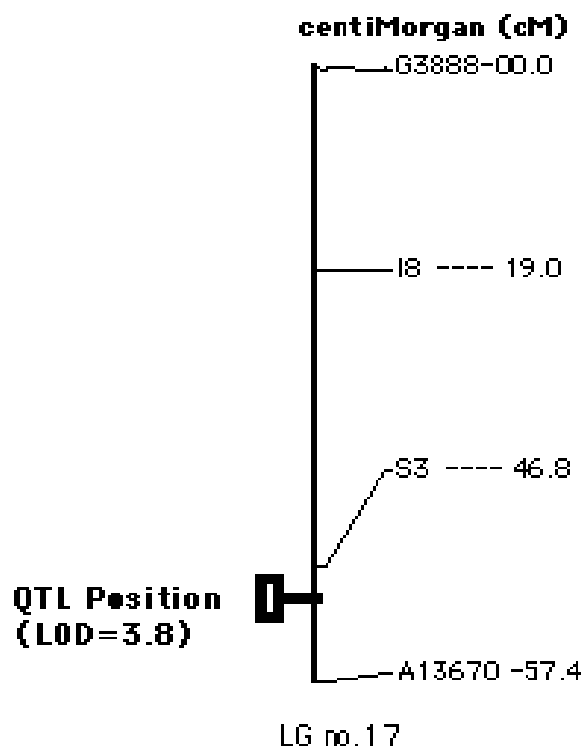
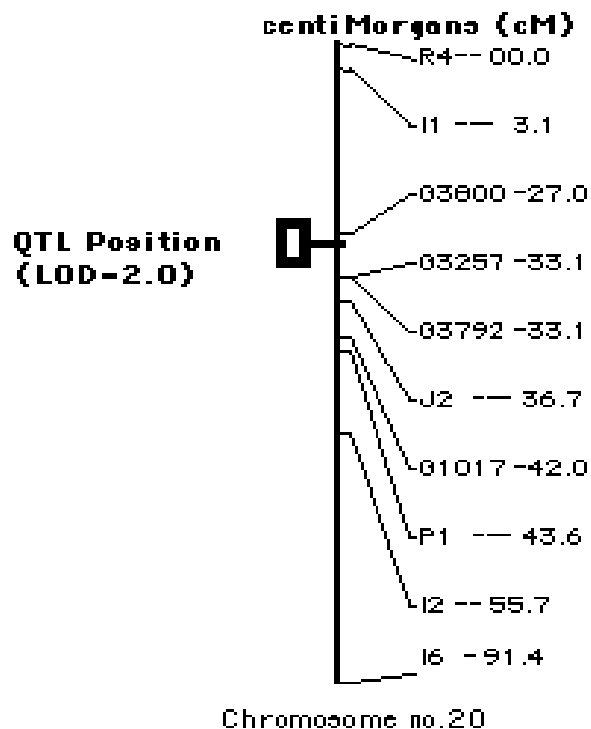


Fig. 3. Location of two putative QTLs for stomatal conductance on cotton chromosome no. 20 and linkage group no. 17. The LOD scores for each QTL were derived from the likelihood ratio test statistic of QTL Cartographer.

detected and located in linkage group 17 and chromosome 20 (Fig. 3). The first putative QTL (LOD = 2.0, LR = 9.2) was located approximately one cM from SSR locus 'G3800' on chromosome 20. The second putative QTL (LOD = 3.8, LR = 17.5) was identified approximately 4 cM from RAPD locus 'S3' on linkage group 17. Molecular markers explained around 12% of variability in stomatal conductance from a multiple regression equation.

The three most informative molecular markers residing near QTL intervals were subjected to single-marker analysis with QGENE (Table 4). The fragment frequency is the mean of stomatal conductance values of $F_{2,3}$ families sharing the same parental allele from each marker. The mean values of stomatal conductance were higher in the dominant (+/-) markers for alleles from upland parent TM1. The phenotypic effects of the TM1 marker allele ranged from 14.8 to 43.8 $\text{mmol m}^{-2} \text{s}^{-1}$. The largest phenotypic effect was observed for S3 among the dominant markers. The mean allelic contribution from the co-dominant SSR marker G3800 at heterozygote (Aa) condition had the highest stomatal conductance mean value, suggesting an overdominance expression for stomatal conductance in this QTL interval.

DISCUSSION

Although TM1 and NM24016 parents were not selected for agronomic characteristics in this study, the expression of the physiological trait of stomatal conductance was related to cotton lint yields in a segregating population from a cross of these two inbred lines. The upland TM1 parent has a higher rate of stomatal conductance than the introgressed NM24016 parent. The present study confirms that high stomatal conductance is associated with high cotton lint yields at supra-optimal temperatures for the cotton crop under irrigated environments. The advantages for this physiological trait would be small or nonexistent in moderate temperate zones, where enhanced evaporative cooling would not be expected to enhance lint yield. The selection for high stomatal conductance may result in retaining higher amounts of the genome from TM1 in the segregating progeny. Certainly upland cultivars are higher yielding than pima in Arizona and New Mexico. If

genes for higher yield were somehow retained in some progeny independent of stomatal conductance, then the yield advantage of those progeny should be realized in Las Cruces and Maricopa. The selected progeny behaved differently in the two environments. Particularly, the selected progeny for lower stomatal conductance were much higher yielding in Las Cruces than in Maricopa (Table 3).

Genetic modifications of the sensory transduction pathway(s) are required in guard cells for genetically stable changes in stomatal conductance (Zeiger, 1983). Stomatal conductance at high temperature was positively correlated with stomatal sensitivity to temperature, and independent from photosynthesis (Lu et al., 1994). In addition, the difference in stomatal conductance between the low- and high-yielding pima lines is under genetic control (Percy et al., 1996). The analysis of quantitative traits is especially interesting to breeders because it opens the door to a more precise manipulation of the trait. Characterization of the relationship between the altered stomatal properties and the attained increases in cotton lint yields and heat resistance has been proposed as a selection criterion in future breeding programs (Lu et al., 1998). However, the strong environmental dependence of stomatal conductance as seen in this experiment and the large number of required measurements may limit breeders' use of stomatal conductance as a selection criterion. The responses for stomatal conductance in the 118 $F_{2,3}$ families as well as in the high and low stomatal conductance $F_{2,4}$ family groups were clear at Maricopa, AZ, where summer temperatures exceed those at Las Cruces, NM.

The QTLs and molecular markers for stomatal conductance provide further evidence for the inheritance of this physiological trait. Compared with conventional methods, QTLs and molecular markers provide breeders new alternatives for selection. Marker-assisted selection can accelerate breeding by reducing the time to develop new cultivars (Tanksley and Hewitt, 1988; Paterson et al., 1991).

The statistical association of a quantitative character with the segregation of a marker gene locus may be the first step in genetic mapping of a locus controlling such a character (Zeng, 1994). Previous work on the inheritance of stomatal conductance in

upland showed additive and dominant variance, with low conductance being dominant (Roark and Quisenberry, 1977).

The inheritance of stomatal conductance in pima varied in complexity from a simple additive-dominance model, to a model displaying digenic epistatic interaction (Percy et al., 1996). In this interspecific population, additive as well as dominant effects for stomatal conductance were observed for the QTLs. The alleles from the dominant markers from the upland parent contributed the highest mean values of stomatal conductance, and further suggest that genes from upland cotton may contribute to the increases in conductance attained in advanced pima breeding lines. The trend observed in these dominant (+/-) markers agrees with previous reports (Lu et al., 1998; Percy et al., 1996; Lu and Zeiger, 1994; Lu et al., 1994; Radin et al., 1994; Cornish et al., 1991).

These results reveal that gene introgression at the DNA level from the upland cotton may contribute to the increases in conductance attained in advanced introgressed pima breeding lines selected for high cotton lint yields and heat resistance at supra-optimal temperatures under irrigated environments (Lu et al., 1998). At the heterozygous state for the SSR marker G3800, the contribution of both parental alleles produces an overdominance effect on the expression of stomatal conductance.

Further research is needed on molecular markers and QTL mapping to screen potential parent lines for stomatal conductance. The polymerase-chain reaction-based markers in this study provide only about 20% coverage of the cotton genome. Much larger numbers of markers are needed to detect all of the QTLs for this trait. Recombinant inbred lines (RILs) have been derived from this population to verify the QTLs for this trait. The divergent-selected progenies can be further evaluated in the RIL population. The introgressed germplasm in this study and the QTLs identified will provide a foundation for future research on this important physiological trait.

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