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Terpenoid Aldehydes in Upland Cottons. II. Genotype-Environment Interactions

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ABSTRACT

Cotton (*Gossypium hirsutum* L.) has unique secondary natural products, sesqui- and sesterterpenoid aldehydes, that have the potential to control phytophagous insect pests, but information on their inheritance has been limited to only one compound, gossypol (G). The objective of this study was to determine genetic and environmental variances and interactions, heritability, and genotypic stability for the major nonvolatile terpenoids in foliar pigment glands. A genotype-by-environment experiment, which included 14 genotypes having from normal to very elevated terpenoid content, was conducted at five diverse Texas locations over 2 yr. Flower buds at the third-grown square stage and first nonglossy terminal leaves were sampled 3 wk after first bloom and analyzed by high performance liquid chromatography (HPLC) for G, *p*-hemigossypol quinone (HGQ), and the heliocides H_1, H_2, H_3, and H_4. Aniline-reaction measurements were made for total flower bud terpenoids. The HPLC data for location means showed differences between the high and low values ranging from eightfold for leaf HGQ to less than twofold for flower bud H_2. Genetic × environment variance components were less than genetic variance components in all instances and were generally very small. Error variance exceeded genetic variance only for HGQ, G, and H_4 in leaves and for H_4 in flower buds. Broad-sense heritabilities averaged 0.46, 0.94, 0.61, and 0.93 for leaves on a plot-basis, leaves on an entry mean-basis, flower buds on a plot-basis, and flower buds on an entry mean-basis, respectively. Stability analyses gave regression coefficients from 0.06 to 2.11 (1.00 defined a stable genotype.) for high-terpenoid lines, whereas commercial cultivars had values from 0.11 to 1.05. Our results indicated that plant breeders and geneticists can select for higher terpenoid levels if this goal is considered desirable in the broad context of increasing cotton host-plant resistance.

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GOSSYPOL (G) and other terpenoid aldehydes are prominent secondary natural products found in Upland cotton (Bell, 1986). Reviews on secondary plant metabolites frequently cite G as a compound that can protect plants against insects (e.g.: Wink, 1988). Research has documented the effect of G as well as related terpenoids on the bollworm/budworm complex (*Heliothis* spp.) and other phytophagous in-

sect pests of cotton (for review: Williams et al., 1987). However, most of this research has stressed the importance of G and neglected the contribution of other terpenoid aldehydes in plant defense against pests. Other terpenoid aldehydes, specifically heliocides and hemigossypolone, were shown to have similar toxicity levels as G, but the relative contribution of these compounds was not clearly determined (Williams et al., 1987).

A simplified host-plant resistance (HPR) concept, centered around G as the chemical basis, has understandably evolved. The various other terpenoid aldehydes have been discovered only in the last decade, and accurate detection methods were not readily available. Chan et al. (1988) have concluded that G has been improperly identified as, "the sole protector-chemical", and they propose a "holistic approach" to HPR, especially for management of *Heliothis*. An integrated approach would specifically include all of the important sesqui- and sesterterpenoid aldehydes found in the pigment glands, and not just G.

In a previous report (Stipanovic et al., 1988), we demonstrated that the standard detection method, the aniline-reaction procedure, did not quantitate terpenoid aldehydes accurately in leaves or flower buds. The aniline method did quantitate total seed terpenoids since G is usually the only measurable terpenoid found in seed glands, and spectrophotometric measurement is possible. For breeders and geneticists who wish to manipulate the terpenoid chemistry of cotton, the important tissues are the plant parts directly under attack from major target pests. The leaves and flower buds are of primary importance for *Heliothis* and other economic pests. The G concentrations in our study were generally less than 10 and 75% of total nonvolatile terpenoids in leaves and flower buds, respectively (Stipanovic et al., 1988). Genetic information is essential for all of the major terpenoids.

Reports of terpenoid inheritance examine only G and are difficult to interpret due to differences in quantitation techniques and interference from other compounds. Stringer and Jones (1987) used generation means analysis of aniline measurements for flower buds from one location with different sampling times and concluded that most of the inheritance was from additive effects or additive × additive epistasis. White et al. (1982a) used generation means analysis from one location to estimate gene action for G in terminal leaves with two chemical methods. The aniline data did not show significant contributions from additive or additive × additive gene action, while dominant and residual epistatic effects were found. The cyclohexane ethyl acetate (CHEA) extract of the phloroglucinol detection for G gave different results, with only significant gene action for additive effects. Estimates of genetic variance and broad-sense heritability were computed for the same experiment and published in another report (White et al., 1982b), but only the CHEA data were used. Although those values were calculated from a single environment with sampling time being the only other factor besides replications, the genetic variance was large, and the heritability estimate was 0.99. Earlier experiments (Lee et al., 1968; Singh and Weaver, 1972; Yang and Davis, 1977; Lee, 1977) used single-environment data and had similar conclusions. Thus, the published literature to date has reported a large proportion of additive genetic variance and high heritability values for G.

The objective of this study was to assess genotype-environment interactions for all major terpenoids in both leaf and flower bud tissues from diverse locations over years. This information should assist cotton breeders and geneticists to evaluate the potential for HPR germplasm enhancement using these important secondary metabolites.

MATERIALS AND METHODS

Fourteen cotton genotypes were planted in a randomized complete-block design with four replicates at each of five Texas locations in 1984 and 1985. Description of statistical design, the five field locations, and chemical analyses for the 1984 field trials have been reported previously (Stipanovic et al., 1988). The experiment was conducted similarly in 1985 except that aniline-reaction analysis was used only for flower bud samples and no seed terpenoid measurements were made. The individual terpenoids in leaves and flower buds measured by high performance liquid chromatography were: (*i*) G; (*ii*) *p*-hemigossypol quinone or 5,8-dihydro-2,3-dihydroxy-6-methyl-4-(1-methylethyl)-5,8-dioxo-1-naphthalenecarboxaldehyde (HGQ); (*iii*) heliocide H_1 or 5,8,8a,9,10,10a-hexahydro-2,3-dihydroxy-7,10a-dimethyl-8-(3-methyl-2-butenyl)-4-(1-methylethyl)-9,10-dioxo-1-anthracenecarboxaldehyde (H_1); (*iv*) heliocide H_2 or 5,8,8a,9,10,10a-hexahydro-2,3-dihydroxy-10a-methyl-4-(1-methylethyl)-7-(4-methyl-3-pentenyl)-9,10-dioxo-1-anthracenecarboxaldehyde (H_2); (*v*) heliocide H_3 or 5,8,8a,9,10,10a-hexahydro-2,3-dihydroxy-10a-methyl-4-(1-methylethyl)-6-(4-methyl-3-pentenyl)-9,10-dioxo-1-anthracenecarboxaldehyde (H_3); and (*vi*) heliocide H_4 or 5,8,8a,9,10,10a-hexahydro-2,3-dihydroxy-6,10a-dimethyl-5(3-methyl-2-butenyl)-4-(1-methylethyl)-9,10-dioxo-1-anthracenecarboxaldehyde (H_4).

The genotypes were chosen specifically to represent a range of total terpenoid content in *G. hirsutum* for an HPR breeding population. Standard cultivars are considered as having a normal nonvolatile terpenoid profile. Three cultivars, Stoneville 213, CAMD-E, and Deltapine 61, were included, which represented diverse elite germplasm. Most reported elevated-terpenoid cotton germplasm originated from a single accession from Socorro Island (TX 934); two germplasm lines, BW76-31-DH (provided by W.P. Sappenfield) and HG6-1-1-144 (provided by R.H. Dilday and developed by M.J. Lukefahr), represented this material. We have released germplasm lines that have elevated-terpenoid content derived from wild accessions other than the Socorro Island line (Altman et al., 1986), and these nine lines, ARSTX-HIGOS 1 through 9, completed the test genotypes.

Each replicate consisted of a two-row plot with rows one meter apart. Row lengths were as follows: Brownsville, TX, 7.6 m; Monte Alto, TX, 9.1 m; Corpus Christi, TX, 6.1 m; College Station, TX, 9.7 m; and Halfway, TX, 7.6 m. Fifty of the first nonglossy terminal leaves and 30 flower buds at the third-grown square size were taken from all replicates 3 wk after the first bloom at that location and prepared as reported (Stipanovic et al., 1988).

A model with random effects was used for analysis as outlined by Comstock and Moll (1963). The Bartlett and Hartley tests (Neter and Wasserman, 1974) were used to measure homogeneity of error variances. As in the initial study (Stipanovic et al., 1988), a logarithmic transformation was warranted to reduce error heterogeneity. Since this procedure greatly reduced the coefficients of variation but did not entirely eliminate error heterogeneity, homogeneous groups of year-locations were used for combined analyses of variance in addition to the complete data set to compare heritability estimates. The ratio of genotypic variance to total phenotypic variance as defined by Comstock and Moll

(1963) was used to estimate broad-sense heritabilities (H) on a mean-basis and plot-basis. Thus,

$$H_{mean} = \frac{\sigma_g^2}{\sigma_g^2 + (\sigma_{gl}^2/l) + (\sigma_{gy}^2/y) + (\sigma_{gly}^2/ly) + (\sigma_e^2/rly)} \text{ and}$$

$$H_{plot} = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{gl}^2 + \sigma_{gy}^2 + \sigma_{gly}^2 + \sigma_e^2}$$

where σ_g^2, σ_{gl}^2, σ_{gy}^2, σ_{gly}^2, and σ_e^2 are estimates of genotypic, genotypic × location, genotypic × year, genotypic × location × year, and error variances, respectively, and where l = locations, y = years, and r = replicates. Approximations of the standard errors for heritability estimates were computed by dividing the standard error for σ_g^2 by total phenotypic variance.

Stability parameters (Finlay and Wilkinson, 1963) were computed for each of the 14 lines. These parameters are regression coefficients (b) for the observed mean at a specific environment regressed on the difference between environment marginal means and the overall mean. Correlation coefficients and deviation mean squares from regression were calculated for the stability parameters as suggested by Lin et al. (1986) to verify the appropriateness of this stability analysis.

RESULTS AND DISCUSSION

The contribution of the other terpenoids relative to G content was substantial for leaves and flower buds

Table 1. Environmental means for terpenoid aldehydes in leaves and flower buds from 14 cotton genotypes grown at five Texas locations in 1984 and 1985.

Compound‡	Environments†												
	1984					1985							
	Bv	MA	CC	CS	Hw	Bv	MA	CC	CS	Hw	LSD	$\bar{X}$	CV
	mg kg^{-1}												%
						Leaves							
HGQ	2 354	5 230	2 900	1 921	856	1996	3 838	2395	5 236	7 161	68	3 389	5.4
G	735	1 039	785	670	413	363	690	429	860	1 019	9	700	3.5
H1	2 188	4 178	3 016	2 146	1 242	1865	2 724	2587	2 147	1 777	30	2 387	3.4
H2	2 583	2 316	2 556	1 887	1 710	1751	2 971	1771	3 475	1 357	21	2 238	2.5
H3	984	1 088	984	771	698	723	1 039	744	1 297	620	9	895	2.8
H4	302	447	549	335	238	323	538	491	494	275	10	399	6.9
TTA	9 156	14 298	10 790	7 730	5 157	7021	11 800	8417	13 509	12 209	97	10 009	2.6
						Flower buds							
HGQ	874	930	1 010	885	692	740	622	927	844	620	13	814	4.2
G	7 071	8 170	10 173	9 279	10 381	2754	3 178	4581	5 027	5 853	49	6 647	2.0
H1	926	1 249	1 174	1 140	873	398	353	1114	478	497	12	820	4.0
H2	1 044	1 012	1 122	1 060	1 067	842	601	1189	664	792	10	939	2.8
H3	425	432	475	450	421	261	228	434	225	255	4	361	3.2
H4	208	256	298	301	192	93	96	101	105	94	8	174	12.6
TTA	10 548	12 049	14 252	13 115	13 626	5088	5 078	8346	7 343	8 111	65	9 756	1.8
ATA	5 344	5 817	6 242	5 987	5 850	4799	4 734	3917	4 560	5 107	23	5 236	1.2

† Bv = Brownsville, MA = Monte Alto, CC = Corpus Christi, CS = College Station, Hw = Halfway. The 1984 data are from Stipanovic et al. (1988); mean ($\bar{X}$), LSD (at the 0.05 probability level), and CV from combined analysis for 1984 and 1985.

‡ HGQ = p-hemigossypol quinone; G = gossypol; H1–H4 = heliocides H_1, H_2, H_3, and H_4, respectively; TTA = total terpenoid aldehydes; ATA = terpenoid estimate by the aniline method.

Table 2. Estimates of variance components and broad-sense heritabilities for leaf and flower bud terpenoid aldehyde content of 14 cotton genotypes grown at five Texas locations in 1984 and 1985.

Compound§	Variance components† (SE)					H‡ (SE)	
	σ_g^2	σ_{gl}^2	σ_{gy}^2	σ_{gly}^2	σ_e^2	plot	mean
				Leaves			
HGQ	82 (36)	0.02 (11.3)	<0	36.6 (16.3)	179 (13)	0.28 (0.12)	0.91 (0.39)
G	30 (13)	<0	<0	10.3 (4.7)	52 (4)	0.33 (0.14)	0.93 (0.38)
H1	139 (56)	1.0 (5.6)	2.2 (4.2)	22.2 (7.8)	68 (5)	0.60 (0.24)	0.96 (0.39)
H2	50 (21)	1.2 (1.7)	3.2 (2.2)	2.1 (2.3)	37 (3)	0.53 (0.22)	0.94 (0.39)
H3	43 (18)	<0	3.3 (2.4)	4.2 (2.7)	36 (3)	0.50 (0.21)	0.94 (0.39)
H4	149 (60)	<0	<0	23.7 (12.8)	159 (11)	0.45 (0.18)	0.96 (0.39)
TTA	70 (29)	<0	1.4 (2.7)	10.4 (5.0)	58 (4)	0.50 (0.21)	0.96 (0.39)
				Flower buds			
HGQ	266 (107)	5.1 (4.1)	5.8 (4.3)	3.9 (4.9)	81 (6)	0.74 (0.30)	0.98 (0.39)
G	94 (38)	0.8 (2.0)	1.2 (1.6)	5.5 (2.7)	32 (2)	0.70 (0.28)	0.98 (0.39)
H1	139 (57)	6.3 (3.1)	5.8 (3.5)	<0	71 (5)	0.63 (0.26)	0.96 (0.39)
H2	85 (34)	3.2 (2.0)	2.2 (1.7)	1.3 (2.2)	38 (3)	0.66 (0.27)	0.97 (0.39)
H3	49 (21)	2.6 (1.6)	4.4 (2.5)	<0	36 (3)	0.53 (0.22)	0.93 (0.39)
H4	95 (59)	36.4 (18.4)	66.2 (33.3)	<0	406 (29)	0.16 (0.10)	0.65 (0.41)
TTA	97 (39)	1.9 (1.8)	1.8 (1.6)	3.1 (2.1)	30 (2)	0.73 (0.29)	0.98 (0.39)
ATA	32 (13)	0.3 (4.1)	0.1 (0.3)	0.2 (0.5)	10 (1)	0.76 (0.30)	0.99 (0.39)

† All variance component estimates are × 10^3 and are calculated from natural log transformation data. σ_g^2 = genetic variance; σ_{gl}^2 = genetic by location interaction variance; σ_{gy}^2 = genetic by year interaction variance; σ_{gly}^2 = genetic by location by year interaction variance; and σ_e^2 = error variance.

‡ H plot = heritability on a single plot-basis, and H mean = heritability on a line mean-basis; negative variance component estimates were assumed to be zero for heritability calculations.

§ HGQ = p-hemigossypol quinone; G = gossypol; H1–H4 = heliocides H_1, H_2, H_3, and H_4, respectively; TTA = total terpenoid aldehydes; ATA = terpenoid estimate by the aniline method.

Table 3. Stability parameters† for terpenoid aldehydes from leaves of 14 cotton genotypes grown at five Texas locations in 1984 and 1985.

Genotype	Terpenoid aldehydes‡						
	HGQ	G	H1	H2	H3	H4	TTA
BW76-31-DH	0.92 (0.19)	0.90 (0.19)	1.03 (0.23)	1.30 (0.14)	1.24 (0.19)	1.59 (0.42)	1.00 (0.26)
HG6-1-1-144	0.74 (0.06)	0.62 (0.06)	0.67 (0.10)	0.84 (0.10)	0.57 (0.30)	0.64 (0.15)	0.64 (0.08)
ARSTX-HIGOS 1	1.22 (0.07)	1.26 (0.07)	1.32 (0.17)	1.05 (0.11)	1.06 (0.14)	1.77 (0.32)	1.21 (0.13)
ARSTX-HIGOS 2	1.10 (0.11)	1.11 (0.12)	1.05 (0.12)	1.17 (0.11)	1.28 (0.13)	1.12 (0.27)	1.18 (0.13)
ARSTX-HIGOS 3	0.84 (0.10)	1.23 (0.09)	1.28 (0.15)	1.04 (0.13)	1.07 (0.15)	0.76 (0.21)	0.98 (0.16)
ARSTX-HIGOS 4	1.12 (0.08)	1.10 (0.11)	1.02 (0.08)	1.32 (0.07)	1.32 (0.10)	1.18 (0.16)	1.14 (0.09)
ARSTX-HIGOS 5	0.92 (0.11)	0.83 (0.12)	0.94 (0.19)	0.92 (0.10)	0.80 (0.13)	0.91 (0.32)	0.82 (0.16)
ARSTX-HIGOS 6	1.33 (0.13)	1.62 (0.12)	1.44 (0.21)	1.17 (0.13)	1.28 (0.17)	1.14 (0.33)	1.37 (0.19)
ARSTX-HIGOS 7	1.28 (0.08)	1.22 (0.09)	1.02 (0.17)	0.87 (0.10)	0.97 (0.16)	0.97 (0.22)	1.25 (0.15)
ARSTX-HIGOS 8	1.42 (0.12)	1.11 (0.11)	1.35 (0.19)	0.99 (0.11)	1.05 (0.13)	1.31 (0.24)	1.42 (0.16)
ARSTX-HIGOS 9	1.58 (0.16)	1.43 (0.19)	1.17 (0.24)	1.18 (0.15)	1.28 (0.20)	1.00 (0.31)	1.46 (0.24)
Stoneville 213	0.72 (0.13)	0.60 (0.10)	0.71 (0.15)	1.05 (0.12)	0.99 (0.14)	0.63 (0.22)	0.74 (0.17)
CAMD-E	0.30 (0.08)	0.38 (0.10)	0.56 (0.12)	0.67 (0.12)	0.59 (0.14)	0.57 (0.17)	0.36 (0.13)
Deltapine 61	0.53 (0.07)	0.57 (0.07)	0.49 (0.07)	0.49 (0.06)	0.54 (0.07)	0.47 (0.11)	0.45 (0.07)

† regression coefficients as described by Finlay and Wilkinson (1963); SE listed in parentheses.
‡ HGQ = *p*-hemigossypol quinone; G = gossypol; H1-H4 = heliocides H_1, H_2, H_3, and H_4, respectively. The TTA = total terpenoid aldehydes.

Table 4. Stability parameters† for terpenoid aldehydes from flower buds of 14 cotton genotypes grown at five Texas locations in 1984 and 1985.

Genotype	Terpenoid aldehydes‡							
	HGQ	G	H1	H2	H3	H4	TTA	ATA
BW76-31-DH	0.99 (0.32)	1.23 (0.11)	1.63 (0.20)	1.00 (0.29)	1.20 (0.26)	1.99 (0.20)	1.29 (0.14)	1.37 (0.16)
HG6-1-1-144	0.67 (0.22)	0.84 (0.05)	0.75 (0.08)	0.78 (0.12)	0.71 (0.05)	0.66 (0.07)	0.81 (0.06)	0.75 (0.06)
ARSTX-HIGOS 1	1.33 (0.35)	1.13 (0.08)	1.11 (0.08)	0.81 (0.15)	0.96 (0.14)	1.26 (0.07)	1.13 (0.09)	1.14 (0.12)
ARSTX-HIGOS 2	2.11 (0.39)	1.26 (0.06)	1.19 (0.10)	1.52 (0.17)	1.46 (0.09)	1.49 (0.09)	1.35 (0.06)	1.26 (0.09)
ARSTX-HIGOS 3	1.56 (0.27)	1.17 (0.04)	1.25 (0.14)	1.13 (0.20)	1.10 (0.15)	1.11 (0.13)	1.22 (0.06)	1.18 (0.11)
ARSTX-HIGOS 4	1.42 (0.19)	1.06 (0.06)	1.16 (0.10)	1.19 (0.15)	1.19 (0.11)	1.31 (0.09)	1.09 (0.07)	0.82 (0.13)
ARSTX-HIGOS 5	0.56 (0.30)	1.06 (0.08)	0.79 (0.10)	0.93 (0.16)	0.79 (0.11)	0.65 (0.07)	0.97 (0.09)	1.13 (0.12)
ARSTX-HIGOS 6	0.06 (0.22)	1.18 (0.10)	1.28 (0.12)	1.01 (0.26)	1.01 (0.15)	1.16 (0.12)	1.18 (0.11)	1.13 (0.12)
ARSTX-HIGOS 7	1.60 (0.20)	0.94 (0.10)	1.07 (0.11)	1.34 (0.17)	1.33 (0.09)	1.36 (0.14)	0.97 (0.09)	0.99 (0.09)
ARSTX-HIGOS 8	1.14 (0.29)	1.14 (0.08)	1.24 (0.08)	1.15 (0.16)	1.07 (0.10)	1.01 (0.08)	1.15 (0.09)	0.98 (0.12)
ARSTX-HIGOS 9	1.17 (0.27)	1.13 (0.05)	1.21 (0.08)	1.07 (0.18)	1.19 (0.13)	1.25 (0.06)	1.17 (0.07)	1.07 (0.11)
Stoneville 213	0.72 (0.39)	0.77 (0.07)	0.57 (0.12)	0.98 (0.28)	0.69 (0.12)	0.43 (0.10)	0.71 (0.10)	0.71 (0.14)
CAMD-E	0.28 (0.18)	0.47 (0.05)	0.35 (0.07)	0.53 (0.13)	0.48 (0.07)	0.25 (0.08)	0.43 (0.04)	0.68 (0.06)
Deltapine 61	0.41 (0.19)	0.66 (0.09)	0.43 (0.11)	0.60 (0.12)	0.82 (0.40)	0.11 (0.13)	0.60 (0.10)	0.73 (0.15)

† regression coefficients as described by Finlay and Wilkinson (1963); SE listed in parentheses.
‡ HGQ = *p*-hemigossypol quinone; G = gossypol; H1-H4 = heliocides H_1, H_2, H_3, and H_4, respectively; TTA = total sesquiterpenoid aldehydes; ATA = terpenoid estimate by the aniline method.

in the 10 environments (Table 1). Aniline-reaction data underestimated total terpenoid concentration in all instances. Some locations had true mean values that were more than twice the aniline terpenoid estimate, but for flower buds at two locations (Brownsville and Monte Alto in 1985), the aniline measurement was less than 10% below the actual terpenoid content. The environmental effect varied for different compounds and plant parts. The HGQ in leaves showed more than an eightfold difference between the high and low environments, whereas H_2 means for flower buds had less than a twofold difference. A majority of genotype-environment interaction mean squares were significant; out of 15 measurements there were significant mean squares in 11, 8, and 5 cases for lines × locations, lines × years, and lines × locations × years, respectively.

These observations suggest that environmental effects influence terpenoid content and that conclusions based on single-location experiments might need to be re-examined. Also, previous inheritance studies with foliar tissues used chemical analyses that could not determine individual terpenoids nor accurately quantitate total-terpenoid content (e.g. Singh and Weaver, 1972; Yang and Davis, 1977; White et al., 1982a, 1982b; Stringer and Jones, 1987). While seed were analyzed by nonspecific methods from single locations (Lee et al., 1968; Lee, 1977), those data are relatively accurate to the extent that seed pigment glands contain only trace amounts of the terpenoids other than G (Stipanovic et al., 1988).

Variance component estimates from this study (Table 2) had some imprecision due to error heterogeneity, but the CV's for the combined analyses were generally low (Table 1). Only HGQ, G, and H_4 for leaves and H_4 for flower buds had larger error variances than genetic variances (Table 2). The environmental interaction components were usually small and did not often exceed twice their standard error. Therefore, high broad-sense heritability estimates on a mean basis were obtained. The heritability estimates from smaller data subsets with homogeneous error variance were in close agreement with the values in Table 2 from the complete data set. These high heritabilities were generally in agreement with earlier results for G (Singh and Weaver, 1972; Yang and Davis, 1977; White et al., 1982b), even though that literature had limitations with measurement methods and estimation of environmental effects.

Closer scrutiny of the heritability values indicated potentially useful information for future breeding efforts. Detection of H_4 was problematic as indicated by

Table 5. Genotypic means for terpenoid aldehydes from leaves of 14 cotton genotypes grown at five Texas locations in 1984 and 1985.

Genotype	Terpenoid aldehydes†						
	HGQ	G	H1	H2	H3	H4	TTA
	mg kg^{-1}						
BW76-31-DH	3670	701	3483	2812	1119	566	12 351
HG6-1-1-144	2589	575	1895	1994	847	320	8 220
ARSTX-HIGOS 1	4135	856	2817	2495	977	509	11 789
ARSTX-HIGOS 2	3605	725	2326	2408	946	394	10 404
ARSTX-HIGOS 3	3454	808	2177	2059	830	356	9 684
ARSTX-HIGOS 4	3894	774	2398	2582	993	439	11 080
ARSTX-HIGOS 5	3552	711	2971	2367	968	451	11 020
ARSTX-HIGOS 6	3981	896	3468	2570	1047	549	12 511
ARSTX-HIGOS 7	3669	735	2286	2414	947	401	10 452
ARSTX-HIGOS 8	3478	633	2797	2128	863	438	10 337
ARSTX-HIGOS 9	4588	810	2969	2570	1024	524	12 485
Stoneville 213	3518	632	1578	2209	851	290	9 078
CAMD-E	1701	456	1214	1572	623	185	5 751
Deltapine 61	1662	498	1084	1180	502	169	5 095
LSD (0.05)	81	11	36	25	11	12	115

† HGQ = *p*-hemigossypol quinone; G = gossypol; H1–H4 = heliocides H_1, H_2, H_3, and H_4, respectively; TTA = total sesquiterpenoid aldehydes.

Table 6. Genotypic means for terpenoid aldehydes from flower buds of 14 cotton genotypes grown at five Texas locations in 1984 and 1985.

Genotype	Terpenoid aldehydes†							
	HGQ	G	H1	H2	H3	H4	TTA	ATA
	mg kg^{-1}							
BW76-31-DH	931	8216	1230	1034	402	270	12 083	5725
HG6-1-1-144	536	5657	611	742	294	116	7 956	4724
ARSTX-HIGOS 1	1184	7903	924	1108	406	211	11 736	5842
ARSTX-HIGOS 2	1396	8071	924	1288	461	206	12 346	5911
ARSTX-HIGOS 3	739	6101	817	853	332	170	9 012	5055
ARSTX-HIGOS 4	1220	8186	986	1221	446	213	12 272	5909
ARSTX-HIGOS 5	579	7030	729	797	311	147	9 593	5438
ARSTX-HIGOS 6	612	7883	1045	932	369	208	11 049	5948
ARSTX-HIGOS 7	1066	6928	906	1207	443	212	10 762	5612
ARSTX-HIGOS 8	833	7343	963	924	364	189	10 616	5614
ARSTX-HIGOS 9	1136	7687	1060	1165	431	211	11 690	5922
Stoneville 213	520	4962	469	782	285	108	7 126	4329
CAMD-E	328	3055	398	559	235	82	4 657	3497
Deltapine 61	266	4012	395	500	256	96	5 525	3745
LSD (0.05)	15	59	14	12	5	10	77	28

† HGQ = *p*-hemigossypol quinone; G = gossypol; H1–H4 = heliocides H_1, H_2, H_3, and H_4, respectively; The TTA = total sesquiterpenoid aldehydes; ATA = terpenoid estimate by the aniline method.

the higher error variances for both leaf and flower bud tissues. Although mean heritabilities were high, the plot heritabilities generally should predict more realistic values for varietal improvement, and some of those heritabilities were low, especially for leaf samples. In leaves, the most abundant compound, HGQ, and the most well-known allelochemical for *Heliothis*, G (Williams et al., 1987), had low heritabilities in comparison to these terpenoids in flower buds. This result might be attributable to prior selection primarily for flower bud gland density in most of the breeding programs that have stressed elevated terpenoids.

Stability parameters were estimated to obtain additional information about the genotype-environment interactions (Tables 3 and 4). Usually, correlation coefficients exceeded 0.85, and deviation mean squares from regression were small, indicating that *b* was a relatively good assessment of stability (Lin et al., 1986). A stable genotype was defined as an entry where $b = 1.0$, i.e. an equivalent response across the environments. The cultivars had *b* values less than 1.00 for nearly all measurements. Stoneville 213 generally had higher *b* values than the other two cultivars.

Some of the "high G" lines tended not to respond in environments that were favorable for terpenoid production, as indicated by lower *b* values for HG6-1-1-144 and ARSTX-HIGOS 5 (Tables 3 and 4). However, several lines, such as BW76-31-DH and ARSTX-HIGOS 2 for flower bud terpenoids (Table 4), had *b* values that were considerably greater than 1.0. This observation suggested that some genotypes had a high capability to synthesize terpenoids in favorable production environments.

Genotypic means can further describe the environmental response indicated by stability values. Finlay and Wilkinson (1963) had defined above average stability as genotypes with a low value for *b*. Their ideal stable genotype would have had a high mean and $b = 0$. Eberhart and Russell (1966) pointed out that means are generally lower when $b < 1.0$, and redefined stability as $b = 1.0$. Genotypic means for the terpenoid aldehydes (Tables 5 and 6) generally fit the pattern emphasized by Eberhart and Russell. The standard cultivars with lower stability values had the lowest terpenoid content; very high *b* values ($>>1.0$) were observed for the genotypes with the highest terpenoid means. Occasionally a different pattern occurred, as in the case of BW76-31-DH for total terpenoid alde-

hydes in leaves (b = 1.00 and a very high mean). The importance of these kinds of genotypic differences will depend on the ultimate objectives of terpenoid breeding programs and on their relevance to specific insect pests.

Overall, our results were favorable from the point of view of applied germplasm enhancement. The potential to utilize terpenoids other than G was unknown since G was assumed to be the only consequential nonvolatile terpenoid in pigment glands. Earlier studies on G also were difficult to interpret because of quantitation techniques. With the exceptions noted above (HGQ and G in leaves and H_4 in leaves and flower buds), our study showed that the terpenoids have enough genetic variance, based on the population represented by these genotypes, to be manipulated readily by plant breeders.

Terpenoid content in leaves and flower buds was influenced by the environment. However, the conclusions from previous literature based on single locations appear to be applicable because environmental variance components were generally smaller than genetic variances. Actual genetic gain would be based realistically on individual plot measurements, so the extremely high heritability values on a mean basis in other reports need to be revised. In summary, the terpenoids as a group can be exploited for HPR if plant breeders determine that a modified chemical profile is a high priority for effective insect control.

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