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Performance and Stability of Doubled Haploid Lines of Upland Cotton Derived via Semigamy[1]

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ABSTRACT

Doubled haploid lines of cotton (*Gossypium hirsutum* L.) derived via semigamy and colchicine doubling from diverse parental strains were evaluated for yield in several year-location environments in Mississippi in 1980 and 1981. Experiments were conducted to determine agronomic performance and fiber properties of 15 doubled haploid lines. Selected doubled haploids, their parental strains, and commercial cultivars were evaluated in 1980 for allelochemic compounds alleged to confer resistance to the tobacco budworm, *Heliothis virescens* (F.). Stability parameters were determined for seed cotton yield and allelochemics using linear regression analyses to estimate regression coefficients (b values) and coefficients of determination (r^2 values). A genotype was considered environmentally stable when a unit change in genotype performance corresponded to a unit change in environmental index. The hypothesis, H_o: $\beta = 1.0$, or no significant difference between the performance of a cotton line and the mean performance of all lines over environments was tested for each strain. Agronomic and fiber traits were improved for some doubled haploids but were inferior for other traits compared with their respective parental strains. Generally, doubled haploid lines were as environmentally stable for yield performance as parental strains. This was also true for within-season variability of allelochemic compounds. Heterogeneity of a strain or cultivar was not an apparent prerequisite for environmental buffering effects. Cumulative expression of genetic traits may play a more important role in maintaining environmental stability than relative heterozygosity.

Additional index words: **Environmental buffering effects, Homeostasis, Genotype × environment interaction, Gene segregation, Genetic complements.**

HAPLOIDS and doubled haploids derived from them have long been recognized as excellent experimental material for cytological, genetic, and biochemical studies, and for breeding purposes (Harland, 1955). Haploid plants in cotton (*Gossypium* spp.) were first detected in 1920 as peculiar types of rogues in 'Sea Island' cotton (*G. barbadense* L.). Many of these haploids (n = 2x = 26) occurred as one or both members of a pair of twin seedlings and were detected by the sporadic occurrence of seeds with two embryos, one of which was much smaller and usually haploid (Harland, 1936).

Use of haploids in cotton has been aided by the discovery and use of semigamy in cotton (Turcotte and Feaster, 1963, 1967, 1969, 1974, 1982; Fallieri, 1977). An effective technique to identify cotton haploids by counting stomatal chloroplasts in young seedlings has been developed (Chaudhari and Barrow, 1975). Artificial doubling of haploids provides a shortcut in isolating homozygous strains from highly heterozygous material. In addition, doubled haploid strains could be used as indicators of the magnitude of environmental heterogeneity (Silow and Stephens, 1944).

In early research, the best doubled haploids of *G. hirsutum*, developed from naturally occurring haploids, were equal to commercial cultivars in lint quality and yield, and did not have a narrow range of adaptation (Meyer and Justus, 1960, 1961). Doubled haploids were similar to their parental cultivars in productivity in crosses, interactions with locations, and type of gene action in crosses. F_1 and F_2 populations from crosses of doubled haploids tended to give more consistent performance over all locations than their doubled haploid parents. However, doubled haploids had no consistent advantage or disadvantage when compared to their respective parental cultivars and were not different from other cotton of similar genetic background (Meredith et al., 1970).

The average performance of a population is important, and residual variability may be advantageous in buffering environmental fluctuations (Hutchinson, 1940). A major goal of breeders is the development of strains which consistently give maximum economic yield across environments. Productivity of a population is a function of its adaptability, which is a compromise of stability and flexibility. In lima bean (*Phaseolus lunatus* L.) populations, genetic diversity and productivity were complexly related while genetic diversity and stability were more simply related. Genetic diversity consistently endowed populations with stability (Allard, 1961). However, stability does not imply general consistency of phenotype in varying environments but rather implies stability for yield and quality of economically important traits. A cultivar can achieve stability in two ways: 1) it may contain a number of genotypes (heterogeneity) each adapted to a somewhat different range of environments, or 2) each individual plant may be well buffered or adapted to a range of environments. The terms population buffering and individual buffering describe these two criteria. Genetically homogeneous populations, such as pure line cultivars or single crosses, obviously depend heavily on individual buffering to stabilize productivity, whereas both criteria are available in genetically heterogeneous populations (Allard and Bradshaw, 1964).

Doubled haploids from each of three American Pima (*G. barbadense*) cultivars and a composite of the three doubled haploids showed that the doubled haploids represented the yielding ability of the respective parent cultivars. Lint yields of the doubled haploids were as stable and predictable as those of the cultivars (Feaster and Turcotte, 1973). Approximately 234 doubled haploids (135 from male gametes, remainder from other sources) of Pima cotton were each shown to be uniform, but traits varied among them. In comparison with checks, the doubled haploids generally yielded equal or less, had equal or better boll properties, but with few exceptions had at least one inferior fiber property (Turcotte and Feaster, 1982).

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Since stability, adaptation, and yields of cotton (*G. hirsutum*) cultivars differ, the use of adaptation and stability parameters in conjunction with yield would be of benefit in evaluations of advanced-strain breeding materials (Bilbro and Ray, 1976).

The concept of a gene pool base, which allows for comparisons over years and sites without regard to particular entries in a sample, has been developed (Pederson et al., 1978). Site means can be used as a basis of comparison. Comparisons can be made between cultivars grown in different nurseries (environments) and even in different years. The gene pool concept makes use of a simple linear regression analysis to estimate the regression coefficient (b) and the coefficient of determination (r^2). Concern regarding the use of a low number of environments for this type of analysis has been reported (Pederson et al., 1978). However, some research indicates the use of as few as three to six environments or environment-type criteria have been acceptable (Mather and Caligari, 1974; Nguyen et al., 1980).

Limited research has been conducted on the performance of doubled haploid strains of American Upland (*G. hirsutum*) cotton, particularly those developed via semigamy. Eight doubled haploids developed via semigamy from intervarietal hybrid strains of *G. hirsutum* have been evaluated for agronomic performance and fiber properties. Traits differed among these doubled haploids, but within variability was almost zero. Competitive phenotypic performance and yield data showed they were as stable and adaptable as their parents (Chaudhari, 1979).

Allelochemic compounds have attracted recent attention of scientists as potential resistance factors to insect pests in major crops. Most research in cotton has focused on quantification of gossypol, condensed tannins, anthocyanin, various secondary compounds, and determinations of their role as plant defense mechanisms. Only recently has variability and genotype × environment interaction of allelochemic compounds been reported (Dilday and Shaver, 1980, 1981; Hedin et al., 1983; Lane and Schuster, 1981; White, 1981; White et al., 1982). Allelochemics of interest have been reported to confer a chemical basis for host-plant resistance to *Heliothis* spp. (White et al., 1982).

The objectives of this study were to determine 1) agronomic performance and fiber properties of 15 doubled haploids produced via semigamy from several diverse American Upland cotton parentages, 2) environmental stabilities for yield of these doubled haploid strains of cotton, and 3) the quantitative levels, environmental stabilities, and within season variability for levels of allelochemic compounds from these doubled haploid strains.

MATERIALS AND METHODS

Haploid plants of American Upland cotton (*G. hirsutum*) in *G. barbadense* cytoplasm were developed at Mississippi State, Miss. between 1977 and 1980. The male parents used to develop paternal haploids by means of semigamy were MO-HG, TX-ORH-55-73 (ORH-55), TX-LY-18-72 glandless, 'Paymaster 303', and a F_1 hybrid ('Carolina Queen' $Sm_1 \times ne_1ne_1ne_2ne_2L^\circ L^\circ$). These male parents were not pure lines. Doubled haploid lines were subsequently produced from various haploids by treating small axillary buds with a 0.5% colchicine salve solution. Doubled haploids (D.H.) derived from respective male parent strains were: 1) D.H. 118, D.H. 121, D.H. 126, D.H. 128, and D.H. 1281 derived from MO-HG; 2) D.H. 70, D.H. 84, D.H. 89, and D.H. 90 derived from ORH-55; 3) D.H. 36, D.H. 40, and D.H. 66 derived from TX-LY-18-72 glandless; 4) D.H. 16 and D.H. 94 derived from Paymaster 303; and 5) D.H. 1 and D.H. 2 derived from the Carolina Queen F_1.

The agronomic performance of the 15 doubled haploids was tested in 1980 at three locations in Mississippi: Mississippi State, Batesville, and Stoneville; and in 1981 at Mississippi State. The doubled haploids, four parental strains, and two commercial checks, 'Deltapine 61' (DPL-61) and 'Stoneville 213' (ST-213), were evaluated in randomized complete blocks with four replications in 1980 and six replications in 1981. Planting dates, soil types, harvest dates, and insect pest pressure are presented in Table 1.

Hand harvested boll samples from each plot were used to determine boll weight, lint percent, and seed index. Earliness was measured as percent first harvest. Fiber samples from Mississippi State and Batesville were analyzed for micronaire, 50% and 2.5% span length (SL), percent fiber elongation (E_1), and fiber strength (T_1).

In evaluations of strains for environmental stabilities for yield, total seed cotton yields at several year-location environments were utilized from Stoneville, Batesville, and two locations at Mississippi State in Mississippi in 1980 and three locations at Mississippi State in 1981. All field tests were randomized complete blocks. Strains × environmental interaction was significant. Therefore, stability parameters using regression analyses based on the gene pool concept (Pederson et al., 1978) were determined for total yield. Environmental index is defined as the mean yield of all strains grown in an environment. Our analyses first included a modification suggested by Mather and Caligari (1974), and utilized by Moll et al. (1978) to determine the suitability of the data for the regression approach to environmental stability. These modified regression analyses involved the mean yield of a cotton strain as the dependent (y) variable and the environmental index as the independent (x) variable (excluding the strain in question) in each year-location environment. The stability parameter regression analyses involved the environmental index means for each year-location environment as the mean of all strains. A regression coefficient (b) was then calculated for each cotton strain over environments. Given the same values for the x and y axis of a graph, one can plot the environmental index for each environment. This results in a line of slope (β) equal to 1.0. The regression coefficient (b) for each strain is compared to this line in a statistical test with the

Table 1. Production conditions for agronomic performance tests of doubled haploids of cotton.

Location	Planting date	Harvest dates 1st	Harvest dates 2nd	Soil type	Insect pest pressure
Mississippi State	9 May 1980	27 Oct.†		‡	none
Batesville	7 May 1980	16 Sept.	7 Oct.	§	none
Stoneville	21 May 1980	11 Oct.	1 Nov.	¶	*Lygus* spp.
Mississippi State	10 June 1981	19 Oct.	6 Nov.	‡	none

† Total harvest only.
‡ Leeper silty clay loam (fine, montmorillonitic, nonacid, thermic Vertic Haplaquepts).
§ Memphis silt loam, 2 to 5% slopes, eroded (fine-silty, mixed, thermic Typic Hapludalfs.
¶ Bosket very fine sandy loam, nearly level phase (fine-loamy, mixed, thermic Mollic Hapludalfs).

hypothesis (H_o) $\beta = 1.0$. In actuality, this is testing the relationships between the yield performance of a given cotton strain across environments compared to the environmental indexes over the same environments. Interpretations of environmental stabilities were based on tests of significance on the regression coefficient (b) and the coefficient of determination (r^2) for each strain.

In cooperative research with White (1981), five doubled haploids derived from MO-HG, three doubled haploids derived from TX-LY-18-72 glandless, and their respective parental strains were evaluated for allelochemic compounds that may confer a biochemical basis for resistance to the tobacco budworm, *H. virescens* (F.). This study was planted in the field at Mississippi State on 9 May 1980 in a randomized complete block with four replications. Terminal leaf tissues (ca. 2.5 cm) were collected from each 9 m, 2-row plot, chilled, transported to the laboratory, and freeze-dehydrated. The tissues were then ground for analytical analyses. Weekly samples were taken over a 10-week period beginning 6 June and ending 22 August. Analytical analyses were conducted for percent tannins (catechin test), percent phenolic compounds, percent gossypol (CHEA test), and percent anthocyanin (7A-3W extract) on a dry weight basis as outlined by White (1981). In this research, the allelochemic data are utilized to determine stability parameters of the doubled haploids and parental strains for quantitative levels of allelochemics over a 10-week growing period based on the gene pool concept. The cotton lines were thus evaluated on a weekly basis for levels of allelochemics and the influence of plant age and genotype.

RESULTS AND DISCUSSION

Agronomic Performance and Fiber Properties

Evaluations of doubled haploid strains (Tables 2 and 3) demonstrated that several doubled haploids were equal to or superior to their parent in yield, boll weight, lint percent, seed index, earliness, and fiber properties. However, certain doubled haploids were inferior to their respective parental strains.

The doubled haploids derived from MO-HG, D.H. 121, and D.H. 128 had significantly larger bolls, increased lint percent and fiber elongation, compared with the parental strain. D.H. 126 had smaller bolls and seed index but a significantly higher fiber strength than MO-HG. D.H. 121 had a significantly higher lint yield than its parental strain. The three doubled haploids (D.H. 121, D.H. 126, and D.H. 128) derived from MO-HG and the parental strain were significantly earlier in maturity than the commercial checks. D.H. 128I showed significantly higher yield, boll weight, and lint percent than its parental strain and was equivalent to the commercial checks in these traits. Doubled haploid 128I was derived initially (by doubling with colchicine) from a haploid branch that exhibited both *G. hirsutum* and *G. barbadense* traits; thus, we believe it to be interspecific in nature. The doubled haploid has the leaf type and color of the *G. hirsutum* parent and a faint yellow petal color from *G. barbadense*. Plant structure resembles that of interspecific cotton hybrids. However, the data for D.H. 128I strongly indicate it is not a normal nuclear F_1 hybrid, since interspecific hybrids usually have lower fiber micronaire and higher fiber elongation and strength. In addition, D.H. 128I did not segregate when self-pollinated and data for selfed progeny were dissimilar to that for the other doubled haploid lines derived from MO-HG. On this basis, D.H. 128I is considered to be a homozygous doubled haploid of interspecific nature with possible chromosome complements of genes from both species. How the interspecific haploid branch may have arisen is not known.

Among the doubled haploids derived from ORH-55, D.H. 84 had the best overall agronomic performance with higher lint percent and yield than the parental strain. Doubled haploids 70 and 90 had longer (50% SL, 2.5% SL) fiber than the ORH-55 parent while D.H. 70 had higher fiber strength.

Table 2. Yield and yield components of 15 doubled haploids and check lines of cotton.

Entry	Boll wt	Lint	Seed index	Lint yield	Percent 1st pick
	g	%	g	kg/ha	
D.H. 121	5.06	35.2	12.8	662	91
D.H. 126	3.66	33.6	11.7	560	90
D.H. 128	4.98	34.8	13.1	610	92
D.H. 128I	5.86	35.8	11.2	855	74
MO-HG	4.55	33.2	12.7	556	84
D.H. 70	4.58	31.3	10.5	564	83
D.H. 84	4.60	35.6	10.2	752	74
D.H. 89	4.44	3.22	10.9	562	82
D.H. 90	4.51	30.2	10.7	600	76
ORH-55	4.45	32.7	10.2	571	77
D.H. 36	5.64	34.9	11.5	695	90
D.H. 40	5.87	36.6	11.4	731	89
D.H. 66	5.77	35.8	11.2	720	89
TX-LY	5.83	36.9	11.5	743	87
D.H. 16	6.46	34.2	14.0	712	76
D.H. 94	5.88	29.4	12.9	679	80
Paym. 303	5.80	33.1	12.9	646	77
D.H. 1	5.07	34.3	10.5	509	81
D.H. 2	5.03	34.5	13.3	656	93
DPL-61	5.58	35.3	11.9	919	74
ST-213	5.70	35.4	11.8	885	70
LSD 0.05	0.33	0.8	0.5	89	5

Table 3. Fiber properties of 15 doubled haploids and check lines of cotton.

Entry	Micronaire	50% SL	2.5% SL	Elongation E_1	Strength T_1
		mm		%	mN/tex
D.H. 121	3.9	14.5	30.2	8.5	233.9
D.H. 126	4.6	13.7	27.2	7.4	256.9
D.H. 128	3.7	14.6	30.4	8.4	224.6
D.H. 128I	4.9	13.9	29.2	5.5	210.8
MO-HG	3.9	14.7	30.0	7.0	231.4
D.H. 70	3.9	14.2	30.1	6.6	214.0
D.H. 84	4.0	13.6	28.7	6.1	204.0
D.H. 89	3.9	13.3	29.1	5.8	203.3
D.H. 90	4.2	13.9	30.0	5.9	209.0
ORH-55	3.8	13.6	29.1	6.2	205.4
D.H. 36	3.5	14.0	29.3	7.9	217.5
D.H. 40	4.1	13.5	26.8	7.5	210.2
D.H. 66	3.6	13.9	29.4	7.9	207.7
TX-LY	3.6	13.9	29.0	7.8	214.4
D.H. 16	4.0	14.6	30.3	6.4	232.9
D.H. 94	3.7	14.7	31.3	7.9	219.2
Paym. 303	3.7	13.8	30.4	6.0	208.8
D.H. 1	4.7	13.9	29.4	5.8	223.3
D.H. 2	3.7	14.6	30.6	8.7	225.5
DPL-61	4.8	15.0	31.5	7.3	223.8
ST-213	4.6	14.5	30.8	6.6	212.4
LSD 0.05	0.2	0.4	0.6	0.4	8.4

Table 4. Regression coefficients, standard deviations, and average correlations for seed cotton yield (kg/ha) of doubled haploid strains over environments.

Strain	$b_{i\bar{i}}$†	$S_i/\bar{S}_{\bar{i}}$‡	$\bar{r}_{i\bar{i}}$§
D.H. 121	0.57 ± 0.34	0.60	0.89
D.H. 126	0.69 ± 0.54	0.83	0.77
D.H. 128	0.59 ± 0.14	0.59	0.94
D.H. 128I	1.17 ± 0.48	1.18	0.90
MO-HG	0.69 ± 0.30	0.72	0.92
D.H. 70	1.06 ± 0.25	1.09	0.94
D.H. 90	1.39 ± 0.33	1.36	0.94
D.H. 84	1.31 ± 0.44	1.30	0.92
D.H. 89	1.39 ± 0.30	1.34	0.94
ORH-55	1.20 ± 0.30	1.25	0.91
D.H. 36	0.76 ± 0.50	0.75	0.89
D.H. 40	0.81 ± 0.49	0.80	0.89
D.H. 66	1.03 ± 0.51	1.00	0.90
TX-LY	1.29 ± 0.56	1.24	0.91
D.H. 1	1.08 ± 0.75	1.30	0.80
D.H. 2	0.61 ± 0.37	0.68	0.88
D.H. 16	1.14 ± 0.26	1.11	0.94
D.H. 94	0.86 ± 0.18	0.83	0.95
Paym. 303	1.24 ± 0.65	1.41	0.89
DPL-61	0.85 ± 0.19	0.82	0.95
ST-213	1.14 ± 0.42	1.22	0.87

† $b_{i\bar{i}}$: Regression of means for the *i*th strain on environmental means excluding the *i*th strain.

‡ s_i: Standard deviation for the *i*th strain over environments. $\bar{s}_{\bar{i}}$: Average of the standard deviations for strains represented in the same environments excluding the *i*th strains.

§ $\bar{r}_{i\bar{i}}$: The average of the correlations for the *i*th strain with each of the others.

No significant improvements in agronomic performance or fiber properties of the three doubled haploids derived from TX-LY were found. D.H. 36 had a significantly lower lint percent while D.H. 40 had a significantly coarser and shorter fiber than the parental strain.

Among the two doubled haploids derived from Paymaster 303, D.H. 16 showed a slightly higher lint yield, a significantly larger boll, and a higher lint percent than Paymaster 303. Lint yield of D.H. 94 was reduced due to a significantly lower lint percent. The 50% SL and fiber strength were significantly improved in both D.H. 16 and D.H. 94 over the parent and D.H. 94 had significantly improved fiber elongation.

Between the two doubled haploids derived from (Carolina Queen $Sm_1 \times ne_1ne_1ne_2ne_2L^\circ L^\circ$) F_1, D.H. 2 (normal leaf) had higher lint yield, finer fiber, higher fiber elongation, and was earlier than D.H. 1.

Yields, boll properties, and seed index of these 15 doubled haploids of American Upland cotton were generally equal to or better than their respective parental strains. Fiber properties varied among doubled haploid lines from those superior to the parental strain to those inferior. This contrasts with the performances of doubled haploid strains of Pima cotton where yield performances were generally the same or less than parental cultivars but fiber properties were often inferior for at least one trait (Turcotte and Feaster, 1982). Our results show that some doubled haploids produced from heterozygous strains of upland cotton may perform as well as or better than the parental strains.

Environmental Stabilities for Yield

Yields of doubled haploid strains grown in five to seven environments and evaluated by regression analyses are given in Tables 4 and 5. Initial regression analyses involved regression coefficients for yield of each strain (*i*th) on environmental index means (excluding the *i*th strain) as shown in Table 4. Average correlations ($\bar{r}_{i\bar{i}}$'s) were generally high, except for D.H. 126 and D.H. 1. The regression coefficients ($b_{i\bar{i}}$'s) are reflected almost directly by $s_i/\bar{s}_{\bar{i}}$'s except for D.H. 126 and D.H. 1. Therefore, the use of environmental index values as means of all strains in each year-location environment was considered valid for further regression analyses, as given in Table 5. However, interpretations of performance for D.H. 126 and D.H. 1 may be somewhat less reliable than other strains. The regression analyses allowed for identification of genotypes that performed well in certain environments, as well as having acceptable average performance. Environmental stability of a genotype may be defined from two viewpoints. First, a genotype may be considered stable when a unit change in genotype performance corresponds to a unit change in environmental index. Secondly, a genotype may be considered stable when it has a consistent performance, regardless of environment. The former concept is utilized for the results reported herein to reflect environmental stability. We would thus select as good performing strains, those with regression b values near 1.0 coupled with small deviations, with the constraint of high yield in favorable and nonfavorable stress environments. Performance of genotypes under stress conditions is generally a critical factor in selection; however, the breeder also wants good performance in high yield potential environments.

Generally, the low and high means of each entry

Table 5. Estimates of doubled haploid strain performance based on regression analyses of seed cotton yield in five, six, and seven Mississippi environments.

Strain	Mean	Range		b ± S_d†	r^2
	kg/ha				
		Five environments			
D.H. 36	1944	1606	2822	0.78 ± 0.51	0.89
D.H. 40	1973	1530	2865	0.84 ± 0.49	0.91
D.H. 66	1954	1443	3141	1.05 ± 0.51	0.94
TX-LY	1929	1173	3303	1.31 ± 0.54	0.95
$\bar{X}$	1965	1267	2970	–	–
		Six environments			
D.H. 121	1958	1401	2803	0.65 ± 0.39	0.84
D.H. 128I	2823	1208	4337	1.30 ± 0.46	0.94
D.H. 84	2508	885	4199	1.43 ± 0.42**	0.96
D.H. 89	2120	547	3855	1.50 ± 0.23**	0.99
D.H. 90	2327	846	4039	1.53 ± 0.23**	0.99
D.H. 16	2383	1235	3890	1.26 ± 0.25*	0.98
D.H. 94	2519	1772	3714	0.96 ± 0.21	0.98
DPL-61	2792	2117	4024	0.94 ± 0.25	0.96
$\bar{X}$	2202	1267	3386	–	–
		Seven environments			
D.H. 126	1779	949	3067	0.75 ± 0.64	0.65
D.H. 128	1839	1345	2716	0.68 ± 0.13**	0.97
MO-HG	1985	1387	3129	0.75 ± 0.39	0.83
D.H. 70	2011	916	3469	1.16 ± 0.33	0.94
ORH-55	2152	726	3831	1.31 ± 0.34	0.95
D.H. 1	2082	580	3884	1.17 ± 0.86	0.71
D.H. 2	1974	1481	2891	0.72 ± 0.34	0.86
Paym. 303	2474	839	3827	1.39 ± 0.63	0.86
ST-213	2755	1548	4555	1.25 ± 0.47	0.90
$\bar{X}$	2184	1267	3386	–	–

*,** The regression coefficient (b) is significantly different from 1.0 at the 0.05 and 0.01 probability levels, respectively.

† Standard deviation of b.

occurred in the poor and favorable yield-potential environments, respectively. However, this was not true of all entries. As a result, certain entries were more variable across environments than other entries, as reflected by deviations from the unit slope.

Entries with b values less than 1.0 had low mean yields essentially equal to or slightly above the low environmental mean (poor yield-potential environment) and high mean yields lower than the high environmental mean (favorable yield-potential environment). This response was typical of strains or cultivars that do not respond well to favorable environments or lose yield in progressively unfavorable environments. Their yield potential is limited, regardless of how favorable the environment becomes. They can be considered stable only with respect to their low response to environmental fluctuations. Doubled haploids 121, 126, 128, 36, 40, 2, and the MO-HG strain showed this type of response. However, except for D.H. 128, these strains had b values that were not significantly different from 1.0. The lowest mean value for D.H. 126 was less than the environmental mean in the poor yield-potential environment. The lowest and highest mean performances of D.H. 128I, D.H. 66, D.H. 94, ST-213, and DPL-61 were generally much higher than the respective environmental means for the low and high yield-potential environments, except for the performance of D.H. 128I in the poor yield-potential environment. This response was typical of strains or cultivars that respond directly to environmental fluctuations. They have high yield potential and do well in response to favorable environmental changes. However, the b values for these strains and cultivars were not significantly different from 1.0. DPL-61, D.H. 66, and D.H. 94 had b values near 1.0. ST-213 and D.H. 128I had b values slightly above 1.0. The lowest mean performances of doubled haploids 84, 89, 70, 90, 1, 16, and the ORH-55, TX-LY, and Paymaster 303 parental lines were generally equal to or less than the environmental mean in the poor yield-potential environment but had increasingly favorable responses to favorable yield-potential environments. However, b values were only significantly greater than 1.0 for doubled haploids 84, 89, 90, and 16.

In simple linear regression analyses, the r^2 gives an indication of the reliability of prediction as well as variability. The range of r^2 values for the 21 entries tested was from 0.65 to 0.99. Yield performances of only D.H. 126 and D.H. 1 ($r^2 = 0.65$ and 0.71, respectively) were not explained well by the linear model.

Doubled haploid strains were usually not different from parental strains in yield stability over environments. D.H. 126 was more variable over environments (low r^2) than the MO-HG parental strain while D.H. 128 was less variable. D.H. 84, 89, and 90 were less stable than their ORH-55 parental strain. The range in performance for these strains showed mean changes in yield performance greater than the mean changes in environment with yields lower and higher than the average for unfavorable and favorable environments, respectively. They had above average yield potential in response to environmental changes. Doubled haploids derived from TX-LY were similar to the parent strain in stability. Doubled haploids derived from Paymaster 303 were more stable than the parent cultivar. D.H. 1 was more variable than D.H. 2.

In evaluations of environmental stabilities of doubled haploids based on regression analyses of yield performance, no major differences in response to variable environments were noted between doubled haploids and parental strains. Some doubled haploids and parental strains had low environmental stabilities, whereas other doubled haploids were as stable as parental strains and commercial cultivars. Doubled haploids 66 and 94 and commercial DPL-61 and ST-213 were superior lines with respect to environmental stability. However, the yield potentials of doubled haploids 66 and 94 were not as high as that of the commercial cultivars. The performance of these doubled haploids enhances the usefulness of semigamy as a practical tool in Upland cotton breeding.

Allelochemic Compounds

Performances of doubled haploid strains for levels of allelochemic compounds were evaluated by regression analyses (Table 6). Results reflect relative variability (r^2) and within-season stabilities of allelochemics during ten weeks of plant growth. We know there was a change in plant allelochemics during this ten week growth period (White, 1981). Weeks were thus treated as environments in time. Since r^2 also gives an indication of the reliability of prediction, it reflects the correlated response in level of an allelochemic compound in a given strain as it changes relative to weekly mean values. Strains were evaluated as two separate groups; group 1 were glanded strains and group 2 were glandless strains.

The b values for percent tannin were not significantly different from 1.0 for any strains evaluated. Tannin levels increased in D.H. 128I, ST-213, and DPL-61 and decreased in D.H. 118, relative to weekly means of all entries. Glanded doubled haploids and the parental strain generally had lower r^2 values than glandless strains.

As expected, very little gossypol was measured in the glandless strains. In glanded strains, percent gossypol increased significantly ($b > 1.0$) for D.H. 128 and decreased significantly for D.H. 128I ($b < 1.0$). Variability was reasonably low for most glanded strains except for ST-213. As with gossypol, very little anthocyanin was measured in the glandless strains. In glanded strains, the response for percent anthocyanin was significantly different from 1.0 for DPL-61 where anthocyanin levels increased relative to weekly means. Responses for percent anthocyanin in D.H. 118 and the MO-HG parental strain were variable.

Responses for percent phenolics were significantly different from 1.0 for D.H. 121, D.H. 126, D.H. 128I, TX-LY, ST-213, and DPL-61. Percent phenolics decreased in D.H. 121 and D.H. 126 and increased in D.H. 128I, ST-213, DPL-61, and TX-LY relative to weekly means. Within-season variability was low and was reflected in the high predictive value for levels of phenolics.

In general, within-season stabilities (responses) for

Table 6. Estimates of doubled haploid strain performance based on regression analyses of various quantified allelochemic compounds (dry wt. basis).

Strain	Mean	Range		b ± s_d†	r^2	Mean	Range		b ± s_d†	r^2
	% Tannin, Catechin Test					% Gossypol, CHEA Test				
Group 1										
D.H. 118	12.12	8.42	14.53	0.71 ± 0.32	0.76	0.40	0.23	0.55	1.16 ± 0.32	0.89
D.H. 121	11.90	7.23	15.57	0.93 ± 0.34	0.83	0.39	0.18	0.59	1.35 ± 0.37	0.90
D.H. 126	11.84	7.33	15.68	0.86 ± 0.57	0.60	0.36	0.22	0.45	0.85 ± 0.25	0.88
D.H. 128	12.64	7.19	15.84	0.89 ± 0.40	0.76	0.38	0.17	0.60	1.42 ± 0.32*	0.93
D.H. 128I	12.76	6.41	17.66	1.24 ± 0.55	0.77	0.26	0.17	0.35	0.57 ± 0.23**	0.80
MO-HG	12.62	7.79	16.10	0.89 ± 0.41	0.76	0.39	0.25	0.51	1.02 ± 0.33	0.86
ST-213	14.27	8.36	17.76	1.26 ± 0.39	0.87	0.34	0.22	0.52	0.86 ± 0.47	0.69
DPL-61	14.53	8.68	18.24	1.23 ± 0.29	0.92	0.24	0.14	0.38	0.78 ± 0.30	0.82
X‡	12.84	7.68	15.41	--	--	0.35	0.21	0.49	--	--
Group 2										
D.H. 36	12.10	6.32	18.88	0.92 ± 0.28	0.87	0.09				
D.H. 40	12.09	5.93	15.82	0.94 ± 0.25	0.90	0.10				
D.H. 66	12.63	5.76	19.31	1.09 ± 0.16	0.97	0.09				
TX-LY	12.01	4.55	18.03	1.17 ± 0.16	0.97	0.09				
ST-7AGN	11.53	4.98	15.83	0.94 ± 0.16	0.96	0.10				
X‡	12.07	5.51	17.49	--	--	0.09				
	% Anthocyanin, 7A-3W Extract					% Phenolics				
Group 1										
D.H. 118	0.60	0.35	0.76	0.72 ± 0.43	0.65	10.06	4.97	16.48	0.82 ± 0.21	0.91
D.H. 121	0.55	0.32	0.77	1.03 ± 0.20	0.95	9.83	5.36	16.95	0.85 ± 0.07**	0.99
D.H. 126	0.57	0.38	0.81	0.88 ± 0.24	0.90	9.32	4.98	14.80	0.74 ± 0.09**	0.98
D.H. 128	0.59	0.41	0.85	0.96 ± 0.28	0.89	10.10	4.79	18.50	0.98 ± 0.06	0.99
D.H. 128I	0.50	0.33	0.76	0.87 ± 0.34	0.82	10.44	4.56	20.00	1.19 ± 0.07**	0.99
MO-HG	0.54	0.37	0.75	0.71 ± 0.48	0.60	10.66	4.76	20.19	1.13 ± 0.18	0.96
ST-213	0.64	0.45	1.00	1.17 ± 0.27	0.92	10.31	5.15	20.13	1.13 ± 0.11*	0.99
DPL-61	0.53	0.23	1.21	1.66 ± 0.65*	0.81	10.37	4.74	21.30	1.16 ± 0.15*	0.98
X‡	0.57	0.38	0.84	--	--	10.14	5.02	18.40	--	--
Group 2										
D.H. 36	0.05					10.18	4.31	21.95	0.93 ± 0.08	0.99
D.H. 40	0.07					10.43	3.90	18.83	0.90 ± 0.14	0.97
D.H. 66	0.06					10.71	4.13	22.97	1.03 ± 0.08	0.99
TX-LY	0.07					11.04	3.79	24.59	1.11 ± 0.04**	1.00
ST-7AGN	0.10					10.65	4.37	23.88	1.03 ± 0.09	0.99
X‡	0.07					10.60	4.15	22.44	--	--

*,** Regression coefficients (b) significantly different from 1.0 at the 0.05 and 0.01 probability levels, respectively.
† Standard deviation of b.
‡ Mean of all strains over the growing season. Range.

allelochemic compounds were similar to environmental stabilities for yield. No apparent differences could be attributed to doubled haploids vs. parental or commercial cultivar material. Percent phenolics differed greatly in response among various strains and cultivars, yet had low variability. Percent gossypol had the highest overall variability of all compounds evaluated. These results for yield and allelochemic compounds indicate that genetic traits and their cumulative expression may play a more important role in maintaining environmental stability than does relative heterozygosity.

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