

Effects of Environment Upon Ovule Abortion in Interspecific F₁ Hybrids and Single Species Cultivars of Cotton¹

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ABSTRACT

High ovule abortion rates (mote production) observed in *Gossypium hirsutum* L. × *G. barbadense* L. interspecific F₁ hybrids (ISH) have generally been attributed to the presence of genetic incompatibilities between the two parent species. Other causes of mote production within *G. hirsutum* and *G. barbadense* cottons are adverse environmental factors. This study was conducted to determine to what degree environment contributes to the large mote numbers observed in ISH, to determine if ovule abortion in ISH is more reactive to environment than in single species cultivars, and to determine if parental combinations might influence hybrid sensitivity to mote production. Data were collected from four ISH and their four parent strains under normal and reduced irrigation regimes at two locations in 1983 and under normal and reduced irrigation regimes on three dates at one location in 1984. The soil at the Maricopa, AZ, location used in both years was a Mohall clay loam, a member of the fine-loamy, mixed, hyperthermic Typic Haplargids. The Safford, AZ, location used in 1983 possessed a fine loamy, mixed, thermic Typic Torrifluent soil type. Measurements made included: potential seed number (determined to be the number of seed plus motes per locule), ovule abortion rate (expressed as the percent of the potential seed number per locule which were motes), and locule weight (grams seed cotton per locule). Significant generation and species differences were noted for all traits measured in both years. Significant generation × environment interactions were obtained for ovule abortion rates in 1983 and for ovule abortion rates, potential seed number, and locule weight in 1984. Interspecific F₁ populations were more reactive to the environment than their parent lines. There appeared to be a species contribution to the hybrids' environmental responses, but little evidence of a cultivar-within-species contribution. Little or no environmental response variation was observed among the ISH populations for the traits measured. An environmental sensitivity for ovule abortion within ISH cottons which appears to be independent of parental contribution was documented.

Additional index words: Mote, *Gossypium hirsutum* L., *G. barbadense* L., Genotype × environment.

THE potential advantages of *Gossypium hirsutum* L. × *G. barbadense* L. interspecific F₁ hybrids (ISH) of cotton (Davis, 1978) have been partially offset by the increased ovule abortion rates of such hybrids when compared to intraspecific hybrids or commercial cultivars (Weaver, 1979). Ovule abortion in cotton produces structures called motes, which vary in size and degree of development (Pearson, 1949). Since cotton fiber is produced on the seed coat, motes represent losses in yield and fiber quality.

The levels of mote production in ISH have been attributed to genetic incompatibilities between the *G. hirsutum* and *G. barbadense* species (Bhardwaj and Weaver, 1984). There is some evidence that propitious parent combinations might alleviate some of the incompatibility (Charyulu et al., 1984). The use of introgressed parents and outcrossing of interspecific F₁ hybrids with their parent cultivars have been suggested as other mitigating measures (Bhardwaj and Weaver,

1984). All cottons produce motes at some level, and ovule abortion, though ultimately determined by genotype, is strongly mediated by environment (Porter, 1936; Pearson, 1949).

The objectives of this investigation were to determine if ISHs are more reactive to the environment than single species cultivars, to what degree environment contributes to the large mote numbers observed in ISH, and if parental combination influences hybrid sensitivity to mote production.

MATERIALS AND METHODS

One *G. hirsutum* cultivar, Deltapine 62 (DPL 62); one *G. hirsutum* experimental strain, AZ-107; and two *G. barbadense* experimental strains, Pima E4 and Pima 81-102 were crossed to produce four F₁ interspecific hybrid populations. Crossing was accomplished by manually emasculating the two *G. barbadense* strains which were then hand pollinated using the two *G. hirsutum* genotypes as male parents. The four parents were chosen to represent a variety of phenotypes (Table 1). The Pima 81-102 strain had been bred in the lower desert valleys of Arizona and was reported (Feaster, personal communication) to possess a degree of heat tolerance. Pima 81-102 was a shorter-statured, earlier-maturing cotton. Pima E4 was considered to possess minimal heat tolerance and to be high-altitude adapted. Under low-altitude hot conditions Pima E4 displayed a late-maturing, tall, excessively vegetative phenotype. The upland strain AZ-107 was a close-fruited, short-statured, early maturing cotton, whereas DPL 62 was a more intermediate maturity cultivar.

The four parents and four ISH populations were planted in five-row plots 9 m long in a randomized, four-replicate, split-plot design at Maricopa in 1984 and in a two-replicate, split-plot design at Maricopa and Safford in 1983. The soil type of the Safford, AZ, location is a fine-loamy, mixed, thermic Typic Torrifluent; and that of Maricopa is a fine-loamy, mixed, hyperthermic Typic Haplargid. The Maricopa location is a lower desert location of 363 m elevation. It is typified by extreme high daytime temperatures which often remain high at night during the fruiting season beginning in July. In 1983 the average daily maximum temperature for Maricopa during July and August was 40.6°C and the daily minimum was 23.7°C. The Safford location is an 884 m valley in close proximity to a 3050 m mountain peak. Daytime temperatures at Safford are generally more moderate and night temperatures cooler than at Maricopa. In 1983 the

Table 1. Height, yield, and earliness performance of cotton parent genotypes over 2 yr at Maricopa, AZ.

Genotype	Plant height 1982 and 1983	Fiber yield 1982 and 1984	Earliness† 1982 and 1983
	cm	g plot ⁻¹	%
Pima 81-102	83.7c‡	2724b	89.3a
Pima E4	182.5a	2098c	40.6c
AZ 107	86.9c	3600a	79.5b
Deltapine 62	101.9b	3844a	80.6b

† Percentage of total yield harvested on an earlier stratified harvest date.
‡ Means followed by the same letter or letters are not significantly different according to Duncan's multiple range test ($P = 0.05$).

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average daily maximum for Safford during July and August was 36.8°C and the minimum was 19.8°C. The irrigation regimes (whole plots) at both locations consisted of a "normal" irrigation which was the schedule followed at the location as needed, and a "stress" irrigation regime in which every other scheduled irrigation was deleted.

In 1983, 10 bolls per plot were harvested from each replication at Maricopa and Safford. In 1984 at the Maricopa location 15 flowers per plot were tagged on year days (YD) 194, 215, and 236. The temperature highs and lows averaged during the 21 days prior to each tagging were 41.1°C and 25.1°C for YD 194, 38.2°C and 23.5°C for YD 215, and 37.6°C and 23.3°C for YD 236. Bolls which matured from tagged flowers were harvested at season's end. The Safford location was not used in 1984.

Ovule abortion, potential seed number, and locule weight were analyzed and reported on a per-locule basis. Potential seed number was the number of motes plus the number of seed per locule. Ovule abortion was expressed as the percentage of the potential seed number which were motes. Motes were determined as described by Pearson (1949). Locule weights were the weight in g of seed cotton per locule. Data were analyzed using a GLM model of analysis of variance due to missing data. Higher order interactions were tested,

Table 2. Main effect and first-order interaction mean squares from the analysis of variance for percentage of motes, potential seed number (seed + motes), and locule weights in 1983 and 1984.

Source	df	Percent motes	Seed + motes	Locule wt.
1983				
Location (L)	1	2 147.7**	0.025	
Replication (Loc)	2	1 035.6*	0.636	
Irrigation (I)	1	166.9	0.268	
L × I	1	97.6	0.167	
Error A	2	23.9	0.440	
Genotype (G)	7	3 570.9**	17.129**	
L × G	7	481.7**	0.310	
I × G	7	279.4**	1.489**	
Pooled Error	535	101.6	0.372	
1984				
Replication (R)	3	311.9	0.756	0.020
I	1	2 223.4	12.558**	0.157
Error A	3	286.8	0.490	0.025
G	7	13 891.5**	46.219**	1.184**
I × G	7	330.1	0.120	0.129*
Error B	42	218.2	0.404	0.041
Date (D)	2	41 961.9**	7.162**	4.921**
D × I	2	208.3	6.024**	0.260**
D × G	14	473.8**	0.603*	0.262**
Pooled Error	575	163.9	0.354	0.054

*,** Mean squares were significant at the 0.05 and 0.01 probability levels, respectively.

Table 3. Orthogonal contrasts of genotype and genotype × environment interaction mean squares for generations, species, cultivars, and hybrids of cotton in 1983 and 1984.

Genotype contrasts	Mean squares									
	1983		1984		Locule wt.	Genotype × location		Genotype × date		Locule wt.
	Percent motes	Seed + motes	Percent motes	Seed + motes		Percent motes	Seed + motes	Percent motes	Seed + motes	
Parent vs. F ₁	23 041.1**	8.24**	71 560.8**	4.12**	1.05**	2 397.9**	0.31	983.8**	1.06*	0.78**
<i>G. barbadense</i> vs. <i>G. hirsutum</i>	693.3**	102.83**	15 356.4**	295.41**	6.85**	264.3	0.23	1 689.8**	0.88	0.17*
<i>G. barbadense</i> parents	298.8	4.82**	494.5	4.77**	0.01	93.1	0.92	146.6	0.29	0.41**
<i>G. hirsutum</i> parents	56.1	0.36	1 915.0**	8.14**	0.93**	351.2	0.30	169.2	0.35	0.06
Pima 81-102 hybrids vs. Pima E4 hybrids	821.2**	1.06	672.7	0.09	0.11	1.5	0.01	412.0	0.16	0.25*
AZ-107 hybrid vs. DPL62 hybrid (Pima 81-102)	218.2	0.69	51.4	0.05	0.09	353.1	0.45	44.4	0.84	0.03
AZ-107 hybrid vs. DPL62 hybrid (Pima E4)	313.9	0.03	218.1	0.01	0.13	73.5	0.01	99.3	0.17	0.02

*,** Mean squares were significant at the 0.05, and 0.01 probability levels, respectively.

and when found to be nonsignificant were pooled into the error terms. A selected orthogonal contrast series was performed on genotypes and genotype × environment interactions. Genotype × environment interactions were graphically illustrated by arbitrarily setting the change for values of all variables to zero at the Safford location in 1983 and on YD 194 in 1984. Increases or decreases in values at Maricopa in 1983 or on subsequent flowering dates in 1984 were plotted as deviations from zero.

RESULTS

Ovule Abortion

Analysis of variance revealed significant genotypic differences for ovule abortion rates (percentage of motes) within years (Table 2). In 1983 significant location effects occurred, but there were no significant irrigation effects. There were significant genotype × location and genotype × irrigation interactions for the percentage of motes in 1983. In 1984 the flowering dates of the harvested bolls had significant effect upon the production of motes. Significant genotype × date interactions occurred for ovule abortion in 1984. Differences in magnitude between main effect and interaction mean squares indicated that straightforward interpretation of main effects could be made with a good degree of certainty.

A series of orthogonal contrasts between selected genotypes revealed significant differences in ovule abortion rates between the parent and ISH and between the two parent species in 1983 and 1984 (Table 3). The F₁ hybrids' mote percentage was more than twice the mean value of the parent generation (mid-parent value) in both years (Table 4). The two *G. hirsutum* parents possessed a lower mote percentage than did the two *G. barbadense* strains. Significant differences were found between the two *G. hirsutum* parents in 1984, with AZ-107 displaying greater mote frequencies than DPL 62. Contrasts among ISH revealed only one significant population difference at the 5% level during the 2 yr. In 1983, F₁ populations having Pima E-4 as the *G. barbadense* parent had significantly lower mote percentages than those populations having 81-102 as a parent.

Orthogonal contrasts of genotype × location interactions for ovule abortion rates were performed in 1983. Contrasts of genotype × date interactions were performed in 1984 (Table 3). In 1983 the only signifi-

icant genotype \times location interaction occurred between the parent and F_1 generations. Mote production in the ISH increased nearly 9% from the Maricopa to the Safford locations, whereas the midparent value changed less than 1% between the same locations (Table 4, Fig. 1). Although the location interaction between the two parent species was not significant at the 0.05 level, the parent species' responses were in opposite directions. The ISH response was in the same direction as that of the *G. barbadense* species. In 1984 two significant genotype \times date interactions for mote percentage occurred. The ISH and the midparent were again found to differ in response (Table 3, Fig. 2). Mote frequency in the F_1 populations decreased 33% be-

Table 4. Species, midparent, and F_1 hybrid means for percentage of motes, potential seed number (seed + motes), and locule weights of cotton at two locations in 1983 and on three dates in 1984.

Year	Trait	Location (1983) Date (1984)	<i>G. barbadense</i>	<i>G. hirsutum</i>	Parent mean	Inter-specific F_1
1983	Percent motes	Maricopa	16.5	10.4	13.4	31.0
		Safford	13.5	11.9	12.7	22.2
	\bar{x}		15.0	11.1	13.0	26.6
		Maricopa	6.96	7.79	7.19	6.86
		Safford	6.43	7.78	7.11	6.87
1984	Percent motes	YD† 194	48.9	28.0	37.9	69.5
		YD 215	23.9	15.4	19.5	50.3
		YD 236	17.9	8.1	12.6	36.8
		\bar{x}	30.2	17.2	23.3	52.2
	No. seed + motes	YD 194	6.64	8.31	7.51	7.06
		YD 215	6.34	8.10	7.25	6.88
		YD 236	6.68	8.67	7.77	7.49
		\bar{x}	6.55	8.36	7.51	7.14
	Locule wt (g)	YD 194	0.66	1.18	0.94	0.54
		YD 215	0.95	1.33	1.15	0.82
		YD 236	0.96	1.45	1.23	1.13
		\bar{x}	0.86	1.32	1.11	0.83

† YD = year day, the chronological numbering of the days of the year beginning 1 Jan.

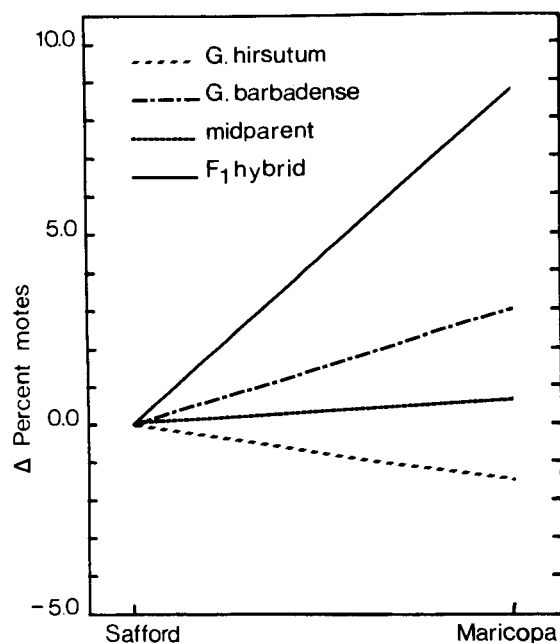


Fig. 1. Change in percentage of motes between Safford and Maricopa in 1983. The change in mote percentages of all populations were set to zero for the Safford location.

tween YD (year day) 194 and YD 236 (Table 4). In the same time period the midparent value changed 25%. The two parent species also responded differently across the three dates. Between YD 194 and YD 236 the frequency of aborted ovules in *G. barbadense* strains decreased 31%, which was only slightly less than the decrease in the ISH. The *G. hirsutum* parents' mote frequency decreased 20% in the same period.

Potential Seed Number

Analysis of variance revealed significant genotypic differences for potential seed number (seed + motes) in both years of the investigation (Table 2). Potential seed number was not affected significantly by irrigation or locations in 1983, nor was there a significant genotype \times location interaction. In 1984 the flowering dates of harvested bolls had a significant effect upon the potential seed number. A significant genotype \times date interaction occurred in 1984.

A series of orthogonal contrasts between selected genotypes revealed significantly different potential seed numbers between the parent and ISH and between the two parent species in both years (Table 3). The F_1 hybrids' potential seed number was lower than the midparent value (Table 4). Within the parent generation, the two *G. hirsutum* parents possessed a larger potential seed number than did the two *G. barbadense* strains. There were significant differences between the two *G. barbadense* strains in both 1983 and 1984. Averaged across years, Pima 81-102 had 0.66 more potential seed per locule than did Pima E-4. In 1984 there were significant differences in potential seed number

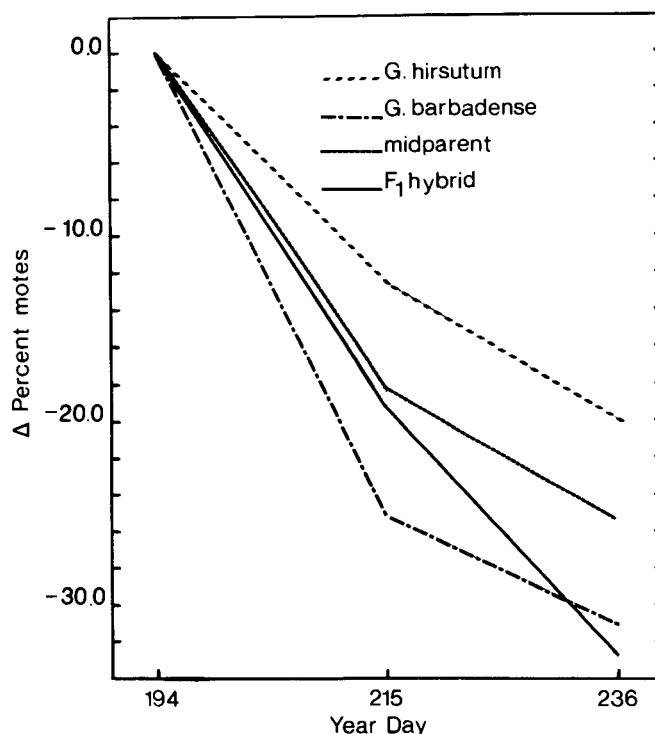


Fig. 2. Change in the percentage of motes over three flowering dates at Maricopa in 1984. The change in mote percentages of all populations have arbitrarily been set to zero on YD 194.

between the two *G. hirsutum* parents; AZ-107 possessed a greater potential seed number than the DPL 62 cultivar. There were no significant differences in the potential seed numbers among ISH populations at the 5% level, despite the significant differences between parent cultivars.

Orthogonal contrasts of genotype \times environment interactions produced no significant interactions for potential seed number in 1983. In 1984 there was a significant generation \times date interaction. The ISH displayed a stronger positive response in seed + motes between YD 194 and YD 236 than did the midparent (Fig. 3). Between those dates the ISH increased in potential seed number by 0.43 seed per locule, whereas the midparent value increased by 0.26 seed per locule. Unlike ovule abortion rates which were unidirectional during the three dates, the potential seed number decreased between YD 194 and YD 215, then increased between YD 215 and YD 236. There were no significant genotype \times date interactions among the populations of the ISH for potential seed number.

Locule Weight

Analysis of variance revealed significant genotypic differences for locule weight in 1984 (Table 2). Locule weights were also affected by flowering dates, but not by irrigation regimes. A significant genotype \times date interaction was obtained.

A series of orthogonal contrasts between selected genotypes revealed significant locule weight differences between the parent and ISH generations (Table 3). The mean locule weight of the ISH was 75% of that of the parent mean (Table 4). Within the parent generation, the *G. hirsutum* parents produced higher locule weights than did the *G. barbadense* strains. There were significant differences between the two *G. hir-*

sutum parents. AZ-107 possessed heavier locules than did DPL 62. No significant differences in locule weights were found among the ISH populations.

Significant genotype \times date interactions occurred between parent and ISH generations, between parent species, and between the *G. barbadense* parent strains (Table 3). The locule weight response of F_1 hybrids between YD 194 and YD 236 greatly exceeded the midparent response or the response of either parent species (Fig. 4). The 0.6 g per locule weight increase of F_1 hybrids over the three dates was twice that of the midparent. This increase also represented a doubling of the ISH locule weight between YD 194 and YD 236. Although the locule weight responses of ISH populations and the *G. barbadense* parent strains were nearly identical between YD 194 and YD 215, these responses diverged greatly between YD 215 and YD 236.

Locule weight provided the only instance in the investigation in which a significant cultivar-within-species response to the environment was convincingly reflected by the ISH (Table 3). The significantly greater locule weight response to the environment of Pima E4 was reflected by the contrast of its ISH response to the response of Pima 81-102 ISH.

There was a close relationship between locule weight and mote percentage in 1984. A negative correlation of 85% was obtained between the two variables.

DISCUSSION

Significant differences for percent motes, potential seed number, and locule weight were found between generations, species, and some cultivars of the investigation. Differences between the parents and ISH were consistent with previous reports (Weaver, 1979; Bhardwaj and Weaver, 1984) of increased mote numbers in *G. hirsutum* \times *G. barbadense* interspecific F_1 hybrids. Observed differences between parent species for potential seed number, locule weights, and mote

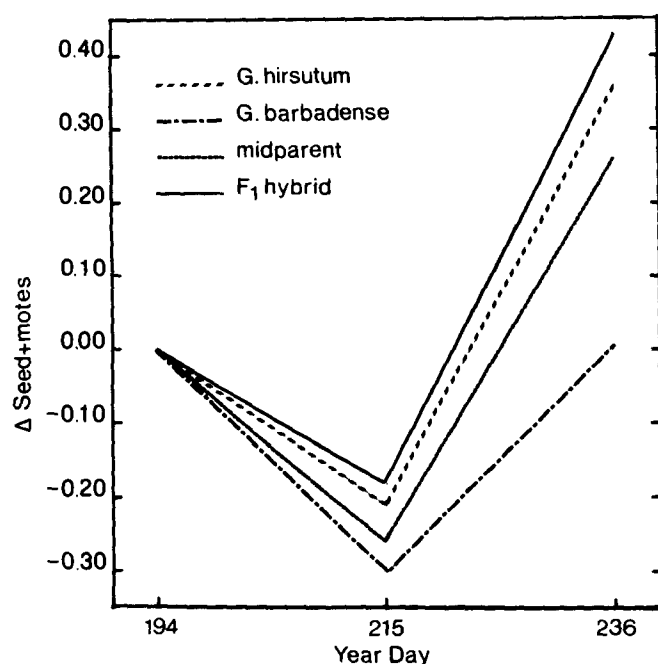


Fig. 3. Change in potential seed number (seed + motes) over three flowering dates at Maricopa in 1984. The change in seed + mote number of all populations has been set to zero on YD 194.

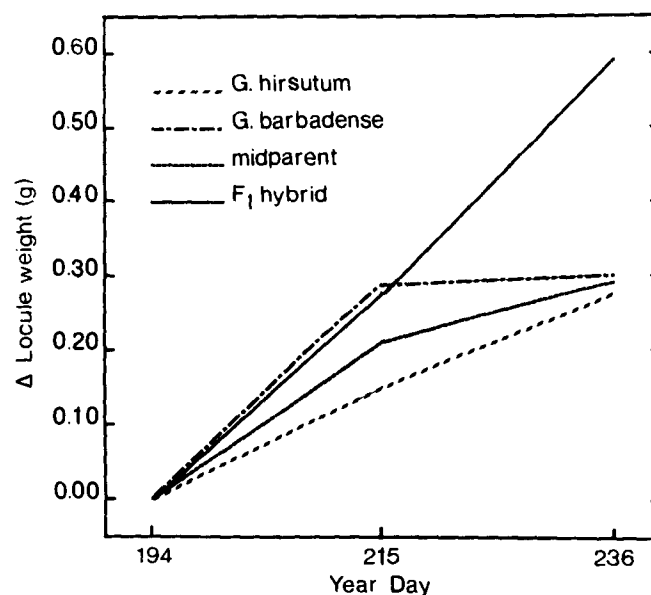


Fig. 4. Change in locule weight over three flowering dates at Maricopa in 1984. The change in locule weight of all populations has been arbitrarily set to zero on YD 194.

percentage were expected. Typically, commercial *G. hirsutum* cultivars produce more seed per locule, have heavier locules, and are less sensitive to environment than are *G. barbadense* cultivars.

Although parent cultivars and strains within species sometimes differed significantly in potential seed number, frequency of motes, or locule weight; there was little evidence that their responses to the environment differed. Parent cultivars and strains in this study had been assumed to represent a degree of physiologic and phenotypic diversity, and their uniform response to the environment was surprising. Only one significant parent cultivar \times environment interaction was observed. This occurred between the two *G. barbadense* parents for locule weight. The heat-tolerant Pima 81-102 strain displayed less response than the more sensitive Pima E-4 during the three observation dates of 1984.

Significant genotype \times environment interactions between parents and hybrids indicated deviations of F_1 hybrids from their midparent responses. The interspecific hybrids' environmental responses generally reflected one parent species or the other, but were often in excess of the parental response. Changes in mote production frequency of hybrids across the two locations of 1983 and three flowering dates of 1984 were similar to responses of the *G. barbadense* parents. In 1983 the hybrids' responses exceeded the *G. barbadense* parents whereas in 1984 their responses were roughly equivalent. Data from 1984 suggested that F_1 hybrids and the *G. hirsutum* parent species responded similarly to flowering dates for potential seed number. One year's data on locule weight indicated that the interspecific hybrids and the *G. barbadense* parents responded similarly to flowering dates for that trait. In 1983 Ano et al. reported several instances of dissymmetry of species effects in hybrids, particularly a preponderant influence of *G. barbadense* upon fiber characteristics. These results were supported by find-

ings of Weaver et al. (1984). It is not startling, therefore, that dissymmetry in species contribution to the ISH extends to environmental response.

In the present investigation, interspecific hybrids' sensitivity to the environment was consistently greater than the midparent response and sometimes greater than either parent species' response. Although there appeared to be a species contribution to the hybrids' environmental responses, there was little evidence of a cultivar-within-species contribution. This result may be due to a general lack of response variability between the cultivars within species used in the investigation. Perhaps if more diverse varieties had been used, stronger cultivar contributions to F_1 performance would have been observed. The interspecific hybrids of the investigation displayed little variability among themselves for environmental response.

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