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Heterosis During the Early Phases of Growth in Intraspecific and Interspecific Crosses of Cotton[1]

A. Marani and E. Avieli[2]

ABSTRACT

The performance of interspecific and intraspecific F_1 hybrids of *Gossypium hirsutum* and *G. barbadense* planted on two different dates was investigated. The interspecific crosses showed significant heterosis for percentage and time of germination, leaf number, and date of square formation when planted on the first planting date, and for plant height, LAI, and dry matter weight for both planting dates. The *G. barbadense* intraspecific cross exhibited a higher degree of heterosis than the *G. hirsutum* one for germination and dry matter weight when planted on the first planting date.

The traits exhibiting significant estimates of heterosis for early planting, but not for late planting, were those associated with the early phases of plant growth. The differences stemming from planting dates were probably due to the low temperature that prevailed after the first planting, since the temperature after the second planting was close to the optimum. We concluded that F_1 hybrids have greater phenotypic stability than their parents when confronted with varying temperature conditions. This condition probably results from their heterosis for seedling growth rate under suboptimal temperature regimes.

Additional index words: *Gossypium*, Planting dates, F_1 hybrids, Germination, Leaf number, LAI, Plant height, Dry matter weight.

HETEROSIS for lint yield and for other traits in cotton hybrids has been reported by several workers (2, 4, 5, 7, 13, 14, 15, 16, 19, 20, 22). The magnitude of this heterotic effect is greater in interspecific crosses between *Gossypium hirsutum* L. and *G. barbadense* L. than in intraspecific crosses among cultivars of each species. In many cases (5, 13, 15, 16, 22) heterosis was also found for plant height, earliness, and other vegetative characters. Excessive plant height is undesirable since it makes mechanical harvesting and insect control more difficult, but vigorous vegetative growth during the early stages of plant development is usually advantageous since it may lead to early flowering and maturity, thus contributing to higher lint yields.

Galal, Miller, and Lee (5) in their study of four intraspecific *G. hirsutum* hybrids found that the rates of seedling growth during the period 30 to 54 days after planting, as well as the rates of dry matter production during the 6th to 9th weeks were greater in F_1 hybrids than in the parental cultivars. This increased growth rate resulted in larger hybrid plants producing a greater yield of fruit. Muramoto, Hesketh, and El-Sharkawy (18) reported that hybrid vigor in an interspecific hybrid between cultivars of *G. hirsutum* and *G. barbadense* was associted with a higher rate of leaf area development. Specific values of leaf area and of dry weight were attained by this hybrid more than a week earlier than by the parental cultivars. However, no differences in net photosynthetic rates between the hybrids and the parental cultivars were detected.

Heterotic phenomena occurring during the initial stages of cotton plant development seem to be of considerable importance. The purpose of the work reported here was to study these phenomena in some interspecific and intraspecific hybrids, planted in the field under two different conditions of temperature, as determined by different dates of planting.

[1] Contribution from The Hebrew University of Jerusalem, Faculty of Agriculture, Rehovot, Israel. Received June 19, 1972.

[2] Associate Professor, Department of Field and Vegetable Crops, and former Graduate Student (Present address: Laboratory of Soil and Water, Yotvata, Doar Eilot).

MATERIALS AND METHODS

The experiment included two *G. hirsutum* cultivars ('Acala 4-42' and 'Acala 1517 C'), two *G. barbadense* cultivars ('Malaki' and 'Pima 32') and the following F_1 hybrids: Acala 4-42 × Pima 32; Acala 1517C × Malaki; Acala 4-42 × Acala 1517C; and Malaki × Pima 32. The first two were interspecific hybrids and the latter two were intraspecific crosses. Plants were grown on irrigated sandy loam soil at Rehovot, Israel. Each of eight cultivars and hybrids was replicated 10 times on each of two planting dates. A separate experiment, designed in randomized blocks, was conducted on each planting date. Each plot consisted of one 2-m-long row, with 1 m between rows. There were 10 equally spaced plants in most of the plots. On the first planting date the seeds were sown in paper pots on April 24 and transplanted to the field after emerging. These paper pots, which were used for the purpose of ensuring a uniform stand of plants, were placed in the same field. At the second planting date seeds were sown directly in the field on July 13.

The number of seedlings that had germinated was counted at 2-day intervals and is expressed as the percentage of the number of seeds sown. The average time of germination was calculated as the sum of the products of the number of seedlings germinated on each day by the number of days after planting, divided by the total number of germinated seedlings. The number of leaves per plant was counted on May 26 and on August 16 on plants planted on the first and second planting dates, respectively. Plant height of three random plants in each of five replicates of each planting date was measured at frequent intervals. The number of plants on which flower buds ('squares') were visible was counted in five replicates of each planting date, on June 10 and on August 29, respectively.

Plants were sampled for dry matter weight and leaf area index determinations four times at 10-day intervals. Sampling started on June 20 and August 26, for the early and late plantings, respectively. Two plants of each of five replicates were taken on each sampling date. Fresh weight of leaf blades and of other plant parts was determined for each sample. A random sample of 50 leaf blade discs (with a total area of 19.24 cm^2) was also weighed for calculating the ratio between leaf area and fresh weight. The leaf area index (LAI) was calculated from these data as described by Watson (21). Plant part samples were oven dried, and their percentage of dry matter was used to calculate the total yield of dry matter in the plants.

RESULTS

The percentage of seeds that had germinated on each day is presented in Fig. 1, and the average time of germination is given in Table 1. On the 6th day after the early planting the parental cultivars had not yet started to germinate, whereas 14% of the *G. hirsutum* and 49% of the *G. barbadense* intraspecific crosses and 53% of the interspecific crosses had germinated. Similar heterotic effects were observed until the 13th day after planting, and the average germination time of the hybrids was shoter than that of the

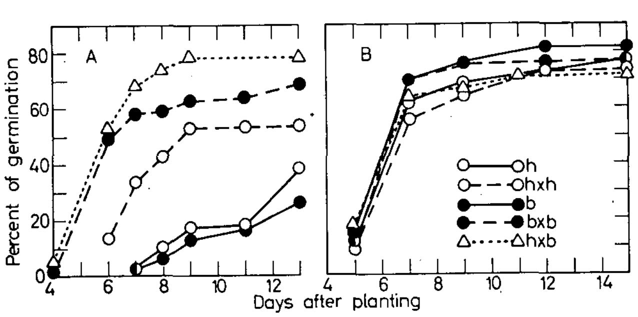

Fig. 1. Percentage of germination of cotton seeds following A — first (April 24) and B — second (July 13) planting: h — *G. hirsutum* parental cultivars; h x h — *G. hirsutum* F_1 intraspecific hybrids; b — *G. barbadense* parental cultivars; b x b — *G. barbadense* F_1 intraspecific hybrids; h x b — Interspecific F_1 hybrids.

Table 1. Average time of germination, number of leaves per plant, and percent of plants with squares of cotton cultivars and their hybrids planted on two planting dates, April 24 and July 13, 1963.

Cultivars and F_1 hybrids	Avg time of germination, days: First planting	Avg time of germination, days: Second planting	Avg number of leaves per plant*: May 26†	Avg number of leaves per plant*: Aug 16‡	% of plants with squares*: June 10†	% of plants with squares*: Aug 29‡
G. hirsutum						
Acala 4-42	10.4	6.2	2.1 c	8.9 a	11 c	87 ab
Acala 1517C	11.3	6.8	2.3 c	8.2 b	2 c	87 ab
Acala 4-42 × Acala 1517C	7.4	6.4	3.2 b	8.0 b	38 b	96 a
G. barbadense						
Malaki	10.8	6.4	2.2 c	6.0 c	0 c	56 c
Pima 32	9.9	5.8	2.0 c	6.5 c	1 c	59 c
Pima 32 × Malaki	6.9	6.0	3.3 b	6.3 c	38 b	61 bc
Interspecific crosses						
Acala 1517C × Malaki	6.4	6.1	3.8 a	8.0 b	75 a	96 a
Acala 4-42 × Pima 32	6.6	5.9	3.8 a	7.9 b	76 a	81 ab

* Results followed by the same letter are not significantly (0.05 level) different by the Student-Newman-Keuls multiple range test. † First planting counted. ‡ Second planting counted.

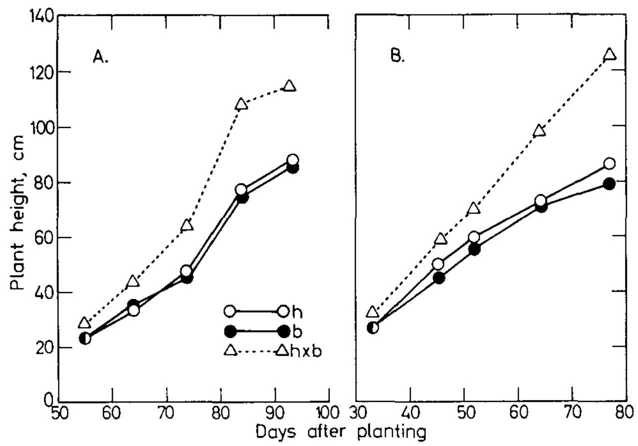

Fig. 2. Height of cotton plants planted on two planting dates, A — first (April 24) and B — second (July 13) planting; h — *G. hirsutum* parental cultivars; b — *G. barbadense* parental cultivars; h x b — Interspecific F_1 hybrids. The intraspecific crosses did not differ significantly from their respective parents.

parental cultivars. No significant differences in germination time or percentage were observed, however, between the parental cultivars and their F_1 hybrids when planted late.

The average number of leaves per plant formed during the 1st month after planting is presented in Table 1. When planted early, the intraspecific crosses formed a significantly greater number of leaves than did their parental cultivars, and the interspecific crosses showed a much higher heterotic effect in this respect. No significant heterosis for this trait was observed, however, following the second planting; the *G. hirsutum* cultivars and intraspecific cross had more leaves than those of *G. barbadense*, and the interspecific crosses had a similar number of leaves as the *G. hirsutum* cultivars.

Plant height measurements are shown in Fig. 2. On both planting dates there was no significant difference between the intraspecific crosses and the parental cultivars of each species, whereas the interspecific crosses were significantly taller than the parental cultivars.

The percentage of plants bearing flower buds ('squares') on the 48th day after planting is presented in Table 1. Considerable heterosis was observed in all the F_1 hybrids that were planted early, especially in the interspecific ones. No significant heterosis was observed for the number of plants bearing squares when plants were planted late.

LAI of the interspecific crosses was significantly higher than that of the parental cultivars after both early and late planting (Fig. 3). LAI of the intraspecific crosses was somewhat higher than that of the parental cultivars, only following early planting but in most cases these differences were not statistically significant.

Dry matter weights of the plants are shown in Fig. 4. The interspecific crosses exhibited a significant heterosis for this trait following both early and later planting. The *G. barbadense* intraspecific cross produced more dry matter than its parents only after early planting, whereas the *G. hirsutum* intraspecific cross did not show any heterosis.

DISCUSSION

Performance of the Different Crosses

It has previously been reported (14) that heterosis for lint yield and for many other traits is much greater in interspecific crosses of cotton than in intraspecific ones. This interspecific heterotic response was found also in the present study for several of the traits that were examined: germination, leaf number, and square formation after early planting; and plant height, LAI, and dry matter weight following both early and late planting.

The *G. barbadense* intraspecific cross exhibited a higher degree of heterosis for some of the traits than did the *G. hirsutum* cross. This difference was statistically significant for the germination and dry matter weight of plants planted in April. A possible reason for this finding might be the divergent origin of the *G. barbadense* cultivars as opposed to the closely related origin of the *G. hirsutum* cultivars used in this experiment. *G. barbadense* cv Malaki is Egyptian and Pima 32 is an American-Egyptian cultivar, whereas the *G. hirsutum* cultivars used were both Acala types. A high degree of heterosis would generally be expected when the parental cultivars have different alleles in a large number of loci, which is usually the case when cultivars are of a divergent origin.

Differences Between the Planting Dates

A significant heterotic effect for several of the traits examined was found after early, but not after late planting. These are all traits associated with the early phases of plant development, i.e., germination, number of leaves 30 days after planting, and number of plants with squares 48 days after planting.

Griffing and Langridge (6), working with *Arabidopsis thaliana* L., found that the heterozygous genotypes exhibited a higher growth rate than the homozygous ones at all temperatures, and a greater stability of phenotypic expression over the entire temperature range (16 to 31 C). This was mainly due to the considerably higher heterotic expression of the hybrids at the higher temperatures. The authors explain the differential heterosis over a range of temperatures by postulating the existence of temperature-sensitive alleles regulating growth rate. McWilliam and Griffing (17) reported similar results for heterosis at different temperatures in maize. They found a higher degree of heterosis for relative growth rate when plants were grown at temperatures higher than the optimum, or following high-temperature shocks, and also when plants were grown at temperatures lower than the optimum.

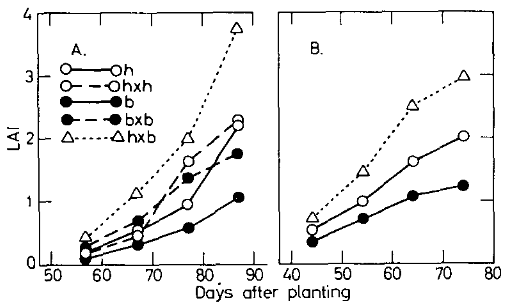

Fig. 3. Leaf area index (LAI) of cotton plants planted on two planting dates, A — First (April 24) and B — second (July 13) planting: h, h x h, b, b x b, h x b — as in Fig. 1. The intraspecific crosses did not differ significantly from their respective parents on the second planting date.

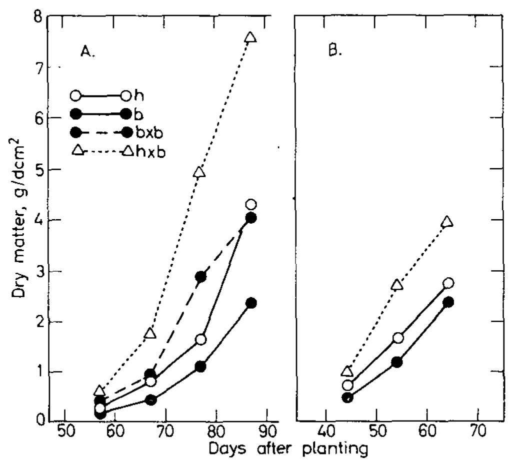

Fig. 4. Dry matter weight of cotton plants planted on two planting dates, A — first (April 24) and B — second (July 13) planting: h, b, b x b, h x b — as in Figure 1. The intraspecific crosses did not differ significantly from their respective parents on the second planting date nor did h x h on the first planting date.

Lewis (11) defined the concept of phenotypic stability as the ratio between the mean values of any character in high- and low-expression environments; a genotype is regarded as "stable" when this ratio is near to unity. He investigated the number of flowers produced by tomato (*Lycopersicon* spp.) plants under two temperature regimes and concluded that the F_1 hybrids have a greater phenotypic stability than the parental cultivars. Lewis (12) also measured the growth rate of an interspecific cross between *Lycopersicon esculentum* and *L. pimpinellifolium,* and found that it was affected by environment (temperature and light) less than the growth rate of the parental varieties. The growth rate of the F_1 hybrid exceeded that of the parental varieties only under extreme environmental conditions such as low temperature and light intensity.

Table 2. Temperatures (Centigrade) during the first 2 weeks after each planting date (weekly averages).

Planting date	Dates	Air temperature Mean	Minimum	Maximum	Soil temperature*
First	April 24-30	18.1	13.0	23.7	22.5
	May 1-7	17.8	11.3	24.1	22.7
Second	July 13-19	25.7	19.2	31.2	31.9
	July 20-26	26.3	21.4	30.9	32.2

* Measured at 0800 hours, at a depth of 5 cm.

Phenotypic stability is frequently defined as the variation between individuals with the same genotype, when they are grown in the same environment or in a random set of different environments. Thus, Williams (23) compared the variability of F_1 hybrids and inbred lines of *L. esculentum* and concluded that there was no difference between them with respect to their ability to buffer or to eliminate the variability that is induced by the environment. Similar results were reported by Jinks and Mather (8) for another inbreeding species, *Nicotiana rustica,* and they concluded that heterozygosity *per* se confers no greater stability of development.

The different heterotic response, that was found in our experiment following the two planting dates was probably due to the low temperature prevailing during the first few weeks following the early planting date (Table 2). The use of paper-pots in the first planting date ensured the achievement of a full stand of plants in the field plots with the limited amount of F_1 seeds available, but it is not probable that this had any effect on the expression of heterosis. Arndt (1) found the optimum temperature for cotton germination to be around 33 C during the first 3 days, and later around 27 C. Camp and Walker (3) reported that this optimum was 33 to 34 C and that the minimum was 14 C. Soil temperatures were therefore very near to the optimum for cotton germination during the first 2 weeks after the second planting date, and much lower than the optimum after the first planting date.

Heterosis was more prominent at the lower temperature of the first planting date than at the optimum temperature of the second one. This result is similar to that reported by Lewis (12) for tomato hybrids, and using his definition of stability it may be concluded that cotton hybrids exhibit a greater phenotypic stability than the parental cultivars. Kohel (9) did not find any clear-cut distinction between the variability of parental cotton cultivars and their F_1 hybrids in a nine-line diallel he investigated, and he concluded that there was no developmental homeostasis associated with F_1 hybrids in cotton. Similar results were found by Kohel and White (10), who also conducted their experiments under field conditions, using only *G. hirsutum* intraspecific crosses with a rather low expression of heterosis.

It may be concluded from our experiments that some cotton F_1 hybrids have a higher phenotypic stability, as defined by Lewis (11), than their parental cultivars. This may be detected when they are grown under unfavorable environmental conditions, especially when using crosses between genetically divergent parents, such as interspecific crosses. A higher degree of heterosis under less-favorable conditions is therefore equivalent, by definition, to a better phenotypic stability of the hybrids.

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