THE GENETICS OF FLOWERING RESPONSE IN COTTON. II. INHERITANCE OF FLOWERING RESPONSE IN A GOSSYPIUM BARBADENSE CROSS[1]

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IN the first paper of this series, LEWIS and RICHMOND (1957) called attention to the renewed scientific interest in the introduction of cotton stocks from tropical centers of variability and reviewed the collecting expeditions that have been made to Mexico and Central America in recent years. More than half of the collected stocks failed to set fruit in the temperate zone during the summer while all of them fruited readily in the greenhouse during the winter. The writers emphasized the fact that in the early development of the agricultural varieties of American Upland cotton, *Gossypium hirsutum*, in the Cotton Belt of the United States, only genotypes which were day-length neutral in fruiting habit persisted longer than the first growing season.

The literature on the physiology of flowering in plants is extensive. It was adequately reviewed by MURNEEK *et al.* (1948) and by LEOPOLD (1951) and by others they cited. Purely genetic studies are less extensive, but the genetic basis of flowering has been recognized since the classic work of GARNER and ALLARD (1920).

Although cultivated stocks of *G. hirsutum* account for almost all of the American cotton crop, cottons with staple lengths of over 1⅜ inches come from varieties of *G. barbadense*. Formerly Sea Island types were important in the Southeastern United States and the West Indies. Currently most American extra-long staple cotton is grown in the irrigated valleys of Arizona, New Mexico and the Trans-Pecos area of Texas. The primitive or semicultivated types of *G. barbadense* are of no less value in the improvement of commercial cottons than the primitive Uplands. Organized collecting expeditions have not been made to the center of variability of *G. barbadense* (the Andean valleys of Bolivia and Colombia) in recent years, but a few *G. barbadense* stocks from these regions have been obtained through colleagues in the United States and certain Latin American countries.

So far, all the *G. barbadense* stocks collected in the tropics exhibit a short-day reaction when grown under the long-day conditions of summer in the American

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Cotton Belt. One such stock PI 220040/CB 2933, was collected in 1954 by H. D. BARKER[3] in the region around Socorro, Department Santander, Colombia. The native name for this cotton was Lengupa, and it was used as the short-day parent in the experiment reported here. The day-neutral parent used in these studies was Pima S–1, the agricultural variety of *G. barbadense* grown in the Southwest. Pima S–1 has a complex genetic background and presumably has some *G. hirsutum* introgression in its pedigree.

PROCEDURE

The original cross between Pima S–1 and Lengupa was made under the direction of THOMAS KERR.[4] The parental F_1 stocks were grown at the tropical cotton garden in Iguala, Mexico, during the winter of 1955–56. Seeds were produced on the parents and the F_1 by controlled self-pollination. Also each parent was backcrossed to the F_1 to produce $F_1 \times$ Pima S–1 and $F_1 \times$ Lengupa seeds. The cotton genetics and breeding unit at College Station, Texas received the seed lots in March, 1956. Individual seeds were started in 6-ounce paper cups in the greenhouse. When approximately two weeks old the seedlings were transplanted to the genetics field nursery. Rows were 40 inches wide and the plants were spaced 24 inches in the rows. The plants were scored for "flowering" and "nonflowering" habit and the number of days from planting to first bloom was recorded for each flowering plant. Selfed seeds were obtained on plants which flowered, and appropriate nonflowering plants were transplanted to 10-inch pots in the greenhouse during the winter of 1956–57 in order to obtain seed for verifying the 1956 results with progeny tests in 1957.

As a precaution the plants were grown in a randomized and replicated design in 1956, but the data were pooled after a qualitative type of inheritance was indicated.

RESULTS

The flowering data for the 1956 planting of parental, F_1, F_2 and backcross material are recorded in Table 1. All plants of Lengupa, the F_1 Lengupa $\times$ Pima S-1 and the first backcross of Lengupa failed to flower or to initiate any visible fruit forms. The F_2 population of 147 plants segregated into two distinct classes in the ratio 3 nonflowering plants: 1 flowering. The backcross to Pima S-1 gave a 1:1 nonflowering to flowering ratio. All the data indicated that flowering was controlled by one gene pair with the flowering recessive to the nonflowering habit.

On the hypothesis that the flowering habit in the material investigated in this experiment is controlled by a single recessive gene, the genotypes and correspond-

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ing phenotypes of the parent stocks and their hybrid progeny may be written as follows:

Lengupa	*F F*	Nonflowering
Pima S–1	*f f*	Flowering
F_1 Lengupa × Pima S–1	*F f*	Nonflowering
F_2 Lengupa × Pima S–1	1 *F F*	Nonflowering
	2 *F f*	Nonflowering
	1 *f f*	Flowering
F_1 × Lengupa	1 *F F*	Nonflowering
	1 *F f*	Nonflowering
F_1 × Pima S–1	1 *F f*	Nonflowering
	1 *f f*	Flowering

TABLE 1

Summary of data on flowering response of six progenies involving Lengupa and Pima S–1 grown during long days of summer, College Station, Texas, 1956

Progeny	No. plants		Chi-square	Mean no. of days to first flower*
	Flowering	Nonflowering		
Lengupa	0	29	—	No flowers
Pima S–1	28	0	—	72.6 ± 0.6
F_1 Lengupa × Pima S–1	0	27	—	No flowers
F_2 Lengupa × Pima S–1	42	105†	$\chi^2(1:3)=1.00$, p=.30–.50	75.6 ± 0.9
F_1 × Lengupa	0	82	—	No flowers
F_1 × Pima S–1	43	44	$\chi^2(1:1)=0.01$, p=.90–.95	74.1 ± 0.7

* Mean of plants which flowered.
† One anomalous late-flowering plant classified nonflowering.

The segregations obtained in the F_2 and the first backcross confirm this hypothesis.

In 1957 additional evidence of a critical nature was obtained from progeny analyses of randomly chosen plants from the backcross and F_2 populations scored in 1956. The results were recorded and analyzed by individual progeny, but the data from appropriate progenies were pooled on the basis of a homogeneous chi-square. The results, supported by data presented in Table 2, are summarized as follows:

Progeny tests of segregates from F_1 × Lengupa: All the plants in the backcross to Lengupa were nonflowering and, on the basis of the hypothesis, either *F f* or *F F* in genotype. Thirteen plants from this population were progeny tested. Segregation, in the ratio of 3 nonflowering:1 flowering, occurred in six of the progenies while no segregation for flowering habit occurred in the remaining seven. *Progeny tests of segregates from F_1 × Pima S–1:* The genotype of all the flowering plants should have been *f f*. All the plants in the progenies of four such plants flowered relatively early and profusely. Nonflowering plants in this population should have been heterozygous for the flowering gene, *F f* in genotype. Segrega-

TABLE 2

Summary of data of flowering response in progeny tests of segregates involving Lengupa and Pima S–1 grown during long days of summer, College Station, Texas, 1957

Progeny tests of segregates from:	No. of progeny	Assumed genotype	No. of plants flowering	Non-flowering	Chi-square (1:3)	Mean no. of days to first flower*
F_1 × Lengupa	6	*F f*	15	74	3.15 p=.05–.10	96.2 ± 1.6
F_1 × Lengupa	7	*F F*	0	103	—	No flowers
F_1 × Pima S–1	4	*f f*	72	0	—	88.2 ± 0.5
F_1 × Pima S–1	5	*F f*	32	110	0.46 p=.30–.50	88.6 ± 0.7
F_2 Lengupa × Pima S–1	6	*F f*	21	64	0.02 p=.50–.95	90.8 ± 0.9
F_2 Lengupa × Pima S–1	2	*F F*	0	29†	—	No flowers
F_2 Lengupa × Pima S–1	4	*f f*	33	0	—	89.3 ± 0.7

* Mean of plants which flowered.
† One anomalous late-flowering plant classified nonflowering.

tion occurred in the progenies of all five plants tested and on the basis of pooled data, segregation was in accordance with theoretical expectations, i.e., 3 nonflowering: 1 flowering.

Progeny tests of segregates from F_2 Lengupa × Pima S–1: As in the cases just summarized, the nonflowering plants in this population were assumed to be *F f* or *F F* in genotype while the genotype of the flowering plants was *f f*. Confirmation of these assumptions was obtained by scoring the F_3 progeny of 12 plants. Of eight nonflowering plants tested, six segregated in a 3 nonflowering: 1 flowering ratio in F_3 and, with one anomalous exception, none of the plants in the remaining two progenies segregated. On the anomalous plant, one flower occurred very late in the season. All the plants in the progenies of four flowering plants tested in F_3 flowered relatively early and profusely.

The mean number of days from planting to first flower of the flowering plants in each population is recorded in the last column of Tables 1 and 2. Comparisons of the mean differences among the populations were made by the *t* test, by the method of comparing groups of unequal size outlined by HAYES and IMMER (1942). In 1956 flowering plants from Pima S–1, F_1 × Pima S–1 and F_2 Lengupa × Pima S–1 flowered in 72.6, 74.1 and 75.6 days respectively. Pima S–1 was significantly earlier than the flowering F_2 segregates at the 0.05 level of significance, but there was no statistical significance in the other comparisons.

As recorded in Table 2, five populations contained flowering segregates in 1957. Comparisons among these means showed that the backcross of F_1 × Lengupa, which flowered in 96.2 days, was significantly later in flowering than the other four populations at the 0.01 level. Among these four populations the F_3 Lengupa × Pima S–1 segregates from nonflowering F_2 plants were slightly later than segregates in the backcross of F_1 × Pima S–1 regardless of whether the first backcross to Pima S–1 plants were flowering or nonflowering.

The 1957 plants flowered approximately two weeks later than the 1956 plants.

This seasonal difference was largely caused by a delay in transplanting in 1957. Ideally seedlings are transplanted when about two weeks old, but heavy rains at transplanting time in 1957 made it necessary to hold the plants in the greenhouse for approximately four weeks. Plants made little growth in the 6-ounce paper cups after two weeks.

DISCUSSION

The genetic study of the short-day, nonflowering response of Lengupa, a noncommercial stock of *Gossypium barbadense*, in a cross with Pima S–1, a day-neutral agricultural variety of the same species, showed that difference in flowering response in this material was controlled by one recessive gene pair.

Plants in this study either flowered profusely or not at all except for the anomalous behavior of two plants. In these two cases, only one flower occurred on each plant very late in the season. In vegetative characteristics the two plants resembled the nonflowering type. These cases of flowering of a "normally" nonflowering stock may be somewhat similar to the findings reported by WADDLE (1954), who studied photoperiodic response of short-day and day-neutral hybrids of American Upland stocks. Weak or sporadic flowering was observed in one of the short-day parental stocks which had not flowered in previous seasons. Further investigations showed that this stock rarely flowered at College Station, Texas, where the main experiments were conducted, but flowered moderately to abundantly at the U. S. Cotton Field Station, Shafter, California. Varying flowering responses were obtained at three other locations. Monofactorial inheritance of the flowering habit was indicated in one of the backcross populations, but there was no evidence of simple inheritance in the other hybrid populations. The experiments demonstrated that "the effects of critical short-day photoperiod can be modified by certain environmental elements other than length of day." WADDLE (1954) also stated that "the results obtained . . . all lend weight to the theory of a physiological system in which the genes controlling fruiting response in a given day length are operative only when other elements of the environment, particularly temperature, are interacting in such a manner as to permit their expression."

LEWIS and RICHMOND (1957) found even less evidence of simple inheritance in a cross of short-day *G. hirsutum* var. *marie-galante* and a day-neutral variety of American Upland cotton. In the first backcross populations the recurrent parent was dominant, and there was no segregation for flowering, i.e., backcrosses to the day-neutral parent all flowered while those to the short-day parent all failed to flower. The F_2 segregated for flowering and nonflowering habit, but the data suggested a quantitative rather than a qualitative mode of inheritance. While the data obtained in the study of two stocks of *G. barbadense* cotton reported here show clearly that flowering response is preponderantly under the control of a single gene pair, there can be little doubt that a more critical study under more controlled environmental conditions would have revealed the presence of modifying genes. In fact the writers, along with most other geneticists, hold that the same

can be said of all cases of so-called simple inheritance. The potency of the modifiers in the *barbadense* material must have been low, but they could have been present in sufficient numbers or potency in the two cases of flowering under discussion to account for the results obtained. At any rate the two plants in question were considered to be nonflowering in respect to the basic gene for flowering response.

Once flowering began, all the plants that flowered did so in a relatively short period. According to the hypothesis that flowering in the *barbadense* material used in this study occurred only in homozygous, *f f*, plants, the mean number of days from planting to first flower would be expected to be the same for flowering segregates in all populations. This was essentially the case although Lengupa and Pima S–1 appeared to differ in certain minor genes which affected time of flowering. These genes apparently accounted for the fact that flowering plants in progeny tests of segregates from the backcross of $F_1 \times$ Lengupa flowered later than those in other populations. By the same token their alleles also could have been responsible for the slightly earlier flowering of plants in the progeny tests of the backcross of $F_1 \times$ Pima S–1. Excepting progeny tests of the $F_1 \times$ Lengupa backcross plants, the greatest difference among other means in 1957 was 2.6 days. The statistical significance assigned to differences in mean flowering periods in two comparisons, other than those involving $F_1 \times$ Lengupa, obviously resulted from the remarkable uniformity in flowering period among the plants in the progenies in question.

The qualitative type of inheritance of flowering response of the *G. barbadense* stocks used in these experiments differed markedly from those obtained in earlier experiments involving stocks of *hirsutum*. In *barbadense*, short-day and day-neutral types were essentially under the control of one gene pair, the remainder of the genetic background having only a minor effect on flowering. However, in *hirsutum*, the complex inheritance patterns obtained in hybrid populations indicated that a number of rather potent genes must have been operating. According to HUTCHINSON, SILOW and STEPHENS (1947), both *barbadense* and *hirsutum* are natural amphidiploids and both originated in the New World. From the results of flowering response studied thus far in this series, it is obvious that the two species must have developed different genetic mechanisms for flowering during the course of their evolution.

SUMMARY

The inheritance of flowering response was studied in a cross between Lengupa and Pima S–1, short-day and day-neutral stocks, respectively, of *G. barbadense* cotton. Under natural long-day conditions of summer growth, difference in flowering response was controlled by one gene pair with the short-day, nonflowering response dominant to flowering.

The gene symbols *F* and *f* are proposed.

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