GYNODIOECISM IN CUCUMBERS[1]

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THE standard cultivars of cucumbers, *Cucumis sativus* L., are monoecious. These monoecious plants are male early in development and female later. The standard races exhibit marked differences in the expression of monoecism, ranging from weak to strong male tendency. Available information suggests that these racial differences reflect genetic variations governing rate of sex conversion during plant development (SHIFRISS 1961).

There exists in cucumbers a rare gene which is often associated with complete femaleness (TKACHENKO 1935), i.e., developmentally persistent gynoecism. Evidence provided by SHIFRISS and GALUN (1956) indicates that this gene does not control gynoecism per se but rather accelerates the rate of sex conversion. This gene was designated *Acr* (SHIFRISS 1961).

It was postulated that two different gynodioecious races might be synthesized in this species by incorporating *Acr* into diverse genetic backgrounds. In a race of weak male background the females would be heterogametic, *Acr acr* females and *acr acr* monoecious, and in a race of strong male background the monoecious would be heterogametic, *Acr Acr* females and *Acr acr* monoecious. In this paper we report on the synthesis and behavior of such races.

MATERIALS AND METHODS

The experimental material was developed by SHIFRISS (unpublished) and the study of this material was carried out cooperatively by the present writers.

Two standard monoecious inbreds of the cultivars Marketer and Tokyo represented the diverse genetic backgrounds. The cultivar Marketer is endowed with a relatively weak male tendency and Tokyo is strongly male. These inbreds were self-reproduced for over 20 generations before *Acr* was substituted for *acr*. The source of *Acr* was the Japanese cultivar Shoigon.

The gynodioecious race of Marketer background is *Acr acr* × *acr acr*. It resulted from nine backcrosses, BC_9, of *Acr acr* plants to Marketer. The gynodioecious race of Tokyo background is *Acr Acr* × *Acr acr*. This race was synthesized as follows. An F_2 generation was obtained by self pollination of *Acr acr* plants of BC_8, *Acr acr* × Tokyo *acr acr*. The three genotypes in this F_2 can be identified readily. Both *acr acr* and *Acr acr* are monoecious but, within a growing season, *acr acr* plants do not reach the strictly female phase and *Acr acr* plants do. *Acr Acr* is gynoecious and plants of this genotype were crossed by *Acr acr* plants of the same F_2. The resulting seed represented the gynodioecious race of Tokyo.

TABLE 1

Developmental sex patterns of individual plants in Marketer Acr acr × acr acr

Plant	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
acr acr																				
1	*	*	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	−	−	+
2	*	(−)	(−)	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	−	−
3		*	(−)	−	−	−	−	−	−	−	−	−	−	−	+	+	−	+	+	−
4	*	(−)	(−)	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+
5	*	(−)	(−)	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
6	*	(−)	(−)	−	−	−	−	−	−	+	+	−	+	−	−	−	+	+	+	+
7	*	−	(−)	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
8	*	(−)	(−)	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+
9	*	(−)	(−)	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+
10	*	(−)	−	−	−	−	−	−	−	+	+	−	−	+	−	+	−	−	−	+
Percent +	0	0	0	0	0	0	0	0	0	30	40	30	30	20	30	30	40	50	50	60
Acr acr																				
1	*	*	*	*	*	(+)	(+)	+	(+)	+	+	+	+	+	+	+	+	+	+	+
2	*	*	*	(−)	(+)	(−)	+	+	+	+	+	+	+	+	+	+	+	+	+	+
3	*	*	(−)	*	*	(+)	*	*	(+)	+	+	+	+	+	+	+	+	+	+	+
4	*	*	*	(+)	(+)	(+)	(+)	(+)	(+)	+	+	+	+	+	+	+	+	+	+	+
5	*	*	*	*	*	*	*	+	+	+	+	+	+	+	+	+	+	+	+	+
6	*	*	*	(+)	(+)	(+)	+	+	+	+	+	+	+	+	+	+	+	+	+	+
7	*	*	*	(+)	(+)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
8	*	*	*	(+)	(+)	(+)	(+)	(+)	(+)	+	+	+	+	+	+	+	+	+	+	+
9	*	*	*	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	+	+	+	+	+	+	+	+	+
10	*	*	*	*	*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Percent +			50	75	100	89	89	89	100	100	100	100	100	100	100	100	100	100	100	100

Sequence of leaf axils along the main stem

Data taken in summer 1962, greenhouse culture, New Brunswick, N.J.
Symbols: *, buds invisible or absent; −, staminate buds; +, pistillate buds; (−) and (+), inhibited buds.

Apart from sex, and its associated effects upon growth and flowering to be discussed later, we were not able to detect any significant differences between plants of the original monoecious inbreds and their comparable gynodioecious races.

The monoecious inbreds and their respective gynodioecious races were grown in different environments. Only one lot of seed of each race was used for planting. Data were obtained on the developmental sex patterns of individuals of each genotype in each environment. Developmental sex patterns are illustrated in Table 1. The sex pattern of an individual plant shows the kind of flower buds which this individual differentiated at sequential leaf axils along the main stem. The sex pattern of a genotype represents the sex patterns of a given number of individuals. This is expressed in percent of individuals which differentiated pistillate buds at each of the sequential leaf axils along the main stem (percent +, in Table 1).

Environment I represents controlled conditions in four growth chambers: (a) photoperiod, 12 hr; (b) light intensity, as measured at the growing apices, increased progressively from 1000 ft-c at seedling stage to 2000 ft-c at maturity, as plants in time grew taller. About 90 percent of the light energy was supplied by Sylvania fluorescent tubes F96T12 CWVHORFL and 10 percent by incandescent lamps; (c) temperature, 24 ± 1°C during the light period and 18 ± 1°C during the dark period as recorded at a given location in the growth chamber. There were, however, marked variations in temperature at different points of each growth chamber, particularly when plants increased rapidly in height.

The seed was germinated at 30°C and seedlings were planted in vermiculite and irrigated with Hoagland #2 nutrient solution. The plants were grown in four replications, each growth chamber being a replication. Each genotype was represented by a total of 32 plants. Initially more plants than needed were grown; when they reached the five-leaf stage sex classification in the gynodioecious races was possible, and plants were randomized.

Environment II represents cultural field conditions at the Agricultural Substation, Lajas, Puerto Rico, from November 30, 1962 to January 31, 1963. The seedlings were grown in sterilized soil in 3-inch peat pots under greenhouse conditions prior to field transplanting. The temperature in the greenhouse exceeded the outside temperature by about 5°C.

In the field the plants were grown in four replications. There were 12 plants per replication for each of the monoecious inbreds of Marketer and Tokyo and 100 plants per replication for each of the gynodioecious races. Although sex patterns were obtained from all plants, the data reported here are based on only 32 individuals, 8 × 4, for each genotype. These individuals were selected at random.

Other environments were: (III) greenhouse conditions of controlled short days, 12-hr photoperiod, and controlled temperatures of 24 ± 1°C to 18 ± 1°C, day and night, during winter of 1963 in New Brunswick; (IV) greenhouse conditions as in III but controlled long days, 16-hr photoperiod, obtained by extending the natural day with light from incandescent lamps which provided about 60 ft-c; (V) greenhouse conditions during summer of 1962 in New Brunswick; and (VI) crowded conditions in the greenhouse during winter 1963 in New Brunswick. In the latter environment the plants were grown closely together in flats rather than separately in large clay pots. Our discussion will be confined mainly to the results obtained in Environments I and II because the variations observed in these environments represent the kind of variations to be expected under a fairly wide range of ecological circumstances.

RESULTS AND DISCUSSION

Behavior of gynodioecious races: It is evident from Figures 1 and 2 that Marketer *Acr acr* × *acr acr* and Tokyo *Acr Acr* × *Acr acr* are basically gynodioecious races. In both races the ratio of gynoecious to monoecious is 1:1 and the sexes can be classified without any difficulty.

Among the nongenetic conditions which affect sex expression in cucurbits, short day, low light intensity (TIEDJENS 1928), and relatively low night tem-
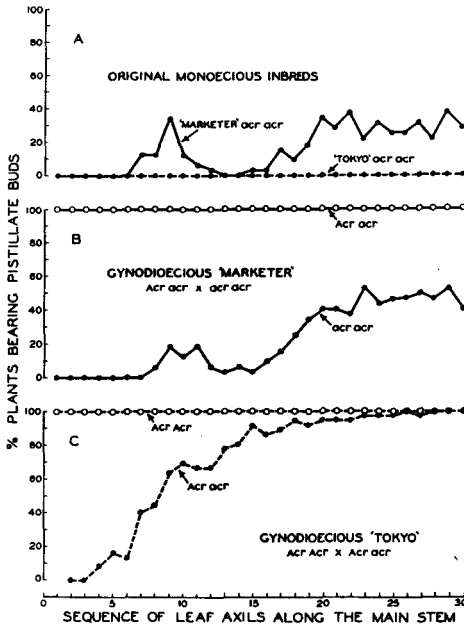
FIGURE 1.—Developmental sex patterns of monoecious inbreds and their respective gynodioecious races grown in Environment I (see text). Each genotype is represented by 32 plants.
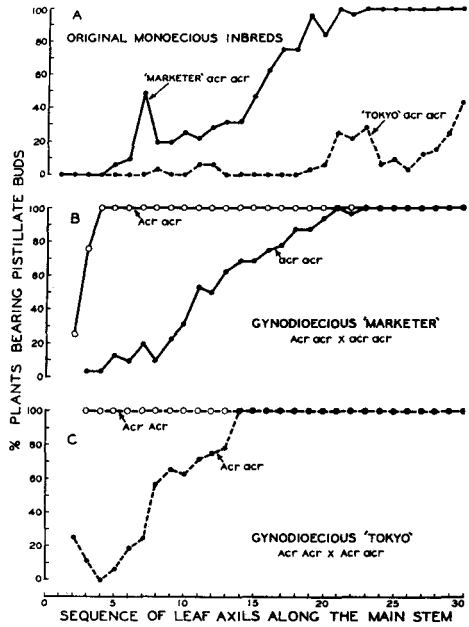
FIGURE 2.—Developmental sex patterns of monoecious inbreds and their respective gynodioecious races grown in Environment II (see text). Each genotype is represented by 32 plants.

peratures (NITSCH, KURTZ, LIVERMAN, and WENT 1952) increase female tendency and the opposite conditions increase male tendency.

Marketer *Acr acr* is essentially gynoecious, but under certain conditions it is prone to differentiate staminate flowers at a few basal leaf axils. It is not known what these conditions are, but our results suggest that high light intensity and high temperature may be contributing factors. Under the conditions of very low light intensity, mostly 500 ft-c, of Environment III (short days) and Environment IV (long days), Marketer *Acr acr* was strictly gynoecist. In contrast, Marketer *Acr acr* differentiated a few staminate flowers under short-day conditions of Environment II (Figure 2B) and under long-day conditions of Environment V (Table 1). The data in Table 1 show clearly that Environment V was conducive to strong male tendency. In contrast, Figure 2A shows that Environment II was conducive to a relatively strong female tendency, but the seedlings in this environment were grown in the greenhouse at high temperatures prior to setting in the field. It may seem strange that Marketer *Acr acr* was strictly gynoecist in Environment I (Figure 1B) in view of the fact that this environment was conducive to a strong male tendency (Figure 1A). However the seedlings in Environment I were grown at light intensity of 1000 ft-c and only later were the plants exposed to progressively higher light intensities.

Tokyo *Acr acr* is monoecious and highly sensitive phenotypically throughout

a long period of plant development. Its behavior in Environments I and II is shown in Figures 1 and 2C. This heterozygote manifests a pulsating pattern during the summer months in New Brunswick, under greenhouse conditions of high fluctuating temperatures. A "pulsating" pattern is a rhythm expressed in several waves of staminate and pistillate leaf axils which alternate each other for some time before the strictly female phase is reached.

Tokyo *Acr Acr* is gynoecious except when crowded in flats (Environment VI). Under such abnormal conditions this genotype differentiates inhibited staminate buds in a few basal leaf axils.

It would be difficult to synthesize phenotypically more stable gynodioecious races from other monoecious cultivars. This is because the expression of *Acr acr* is highly fluctuating, ranging from gynoecism to monoecism, in a genetic background intermediate between Marketer and Tokyo.

A new gynodioecious race of different constitution and sexuality has been synthesized in our laboratory (SHIFRISS, unpublished): *Acr Acr G g × Acr Acr g g*, where *G* is for pistillate flowers and *g* for perfect flowers. In this race the sexes are gynoecists and hermaphrodites. The synthesis of hermaphroditism was reported by SHIFRISS and GALUN (1956).

Dwarfism associated with Acr: Marketer *Acr acr* was significantly shorter in plant height than Marketer *acr acr* in Environments I and III (Table 2). There were no significant differences in plant height among the three genotypes *Acr Acr, Acr acr*, and *acr acr* of Tokyo grown under identical conditions. The circumstances which favor dwarfism in Marketer *Acr acr* are short days and relatively low light intensity. In our experiments, neither short photoperiodism nor low light intensity alone was effective. Dwarfism in this case could be governed by genetic and environmental factors which raise the relative concentration level of native auxins above the range associated with normal internode elongation. This hypothesis is amenable to experimental testing.

Inhibition of flower buds in relation to dosage of Acr: Any plant of the common monoecious cultivars may be looked upon as a single inflorescence, because most leaf axils differentiate flower buds. Inhibition of flowering, however, does exist in some basal leaf axils. A few of these leaf axils do not differentiate flower buds, and others differentiate inhibited flower buds which fail to reach anthesis.

Table 3 shows that in Tokyo *acr acr, Acr acr,* and *Acr Acr* the percent of flower-inhibited leaf axils increases appreciably as the dosage of *Acr* increases

TABLE 2

Plant height in Marketer Acr acr × acr acr

Environment	Number of plants per genotype	Mean height (cm)		F values
		Acr acr	*acr acr*	
I	8	74.4 ± 20.7	139.6 ± 23.2	36.00*
III	10	70.8 ± 35.8	166.0 ± 17.3	64.88*
IV	10	131.3 ± 34.8	145.9 ± 35.8	0.88†

* Significant at 0.01.   † Not significant.

TABLE 3

Inhibition of flower buds in plants of Tokyo background

Genotype	Number of plants	Number of leaf axils*	Number of flower-inhibited leaf axils	
acr acr	48	1440	69	(4.8%)
Acr acr	202	6060	830	(13.7%)
Acr Acr	198	5940	1779	(29.8%)

* Thirty sequential leaf axils per plant. Plants were grown in Lajas, Puerto Rico, in 1962–1963.

from zero to two. The developmental phase of flower inhibition is considerably longer in *Acr acr* and *Acr Acr* than in *acr acr* (Figure 3), but it corresponds to the strictly male phase of *acr acr*. The same situation exists in Marketer. Table 1 shows that in Marketer the strictly male phase in *acr acr* and the flower inhibition phase in *Acr acr* end essentially at the tenth leaf axil. It is also evident from Table 1 that the onset of flowering is delayed in *Acr acr* as compared with *acr acr*. Thus, phenotypically *Acr* appears to delay the onset of flowering and to accelerate the rate of sex conversion.

Sex differentiation in individual plants: The common sex pattern of Marketer *acr acr* is illustrated in Figure 2A. This pattern obscures two significant facets of sex differentiation in *individual* plants (Table 1): (1) there is a marked difference between individual phenotypes (Table 1, *acr acr*, Plants 8 and 9); and (2) the conversion from the strictly male to the strictly female phase may be either gradual or abrupt with no transitional stages.

Similar differences among individuals were observed repeatedly in offspring obtained from a single fruit of our Marketer *acr acr* inbred which was self-repro-
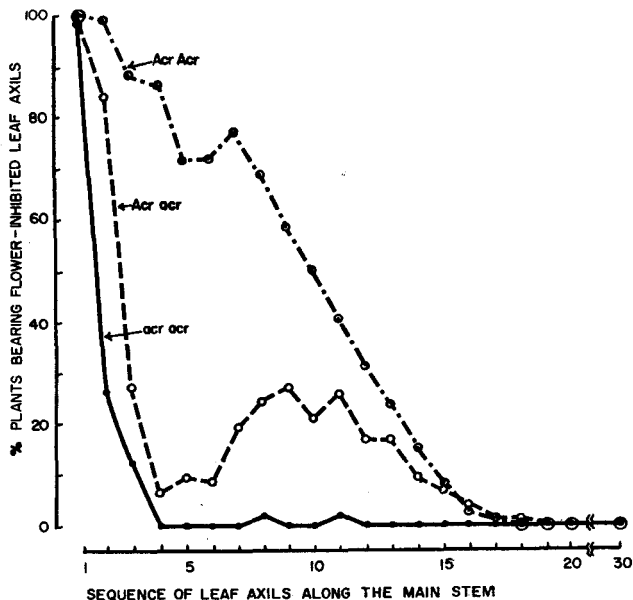

FIGURE 3.—Flower inhibition as related to development and dosage of *Acr* in plants of Tokyo background. Based on data presented in Table 3.

duced for over 20 generations. It is not unusual to find two individuals as different as Plants 8 and 9 (Table 1, *acr acr*) growing side by side in the same nutrient medium and under identical conditions of light and temperature. The existence of such marked differences among *acr acr* individuals reflect the potential variations of a given genetic background. These potential variations may have bearing upon the fluctuating expressivity of *Acr acr* in some genetic backgrounds.

Evolution of dioecism: The synthesis of fairly stable gynodioecious races may be regarded as a step in the evolution of dioecism in this species. We have some experimental evidence which indicates that a true dioecious race could be developed from one of our gynodioecious lines through the use of available genes for determinate habit of growth and strong inhibition of laterals. Such genes may transform monoecists into strictly males. The gene for determinate habit eliminates the female phase from the main stem. Complete inhibition of laterals is essential, because branches of monoecists exhibit a stronger female tendency than the main stem and some branches are strictly female. Thus, dioecism might be synthesized in this species through the use of *Acr* and the genetic trimming of plant architecture.

SUMMARY

The standard monoecious cultivars of *Cucumis sativus* L. are male early in plant development and female later. Some cultivars such as Marketer exhibit weak male tendency, and others such as Tokyo are strongly male. There exists a rare gene *Acr* which accelerates the rate of sex conversion during development, thereby decreasing male tendency.

Two different gynodioecious races were synthesized by incorporating *Acr* into the genetic backgrounds of Marketer and Tokyo. These races are: Marketer *Acr acr* females × *acr acr* monoecious and Tokyo *Acr Acr* females × *Acr acr* monoecious.

Gene *Acr* brings about changes in growth habit and flowering: (1) Marketer *Acr acr* is dwarf in short days and low light intensity; and (2) in both genetic backgrounds the incidence of flower inhibition increases as the dosage of *Acr* increases from zero to two. The length of the developmental phase of flower inhibition in *Acr Acr* and *Acr acr* corresponds to the length of the strictly male phase in *acr acr*.

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