

## ANDROECIOUS STRAINS OF *CUCURBITA PEPO* L.<sup>1</sup>

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### INTRODUCTION

Sexuality of the *Cucurbita* species accounts for their unique standing as a monomorphic genus in the *Cucurbitaceae* family. In previous years no plants other than monoecious in habit were known in this genus. Varying proportions of staminate and pistillate flowers as well as their distribution on the plant have so far been the sole differences in sexuality occurring in various species and varieties of the genus *Cucurbita*.

In consequence, research carried out until the present with sex expression in these plants was limited to a determination of genetic and non-genetic factors governing these distinctions (Whitaker, 1931; Nitsch *et al.*, 1952; Wittwer and Hillyer, 1954; Hopp, 1962).

The present study has been devoted to the genetic constitution of androecious plants which represent a newly discovered sex type so far unknown in *Cucurbita*.

### MATERIAL AND METHODS

Androecious plants were found in the progeny of a self-pollinating variety „Greckie” of the *Cucurbita pepo* species, in 1965. The discovery having taken place towards the end of the growing season, that same year it was not possible to cross them with normal monoecious plants. Nevertheless, selfing of two monoecious specimens of the progeny in question afforded some seeds which were planted out in the coming year.

Offspring of one of the selfed plants was entirely monoecious, while the progeny of the other segregated into monoecious and androecious in a ratio 3 : 1, more or less. Tentative examination of the sexuality resulted in setting aside fourteen monoecious plants denoted by symbols D1 to D14 (Table 1). Every one of these plants was self-pollinated and at the same time crossed with various, selected androecious plants.

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Table 1. Genetic Relations which Illustrate the Inheritance of Maleness in *Cucurbita pepo* Cultivated in the Field in Summer of 1967 and in 1968

Monoecious plants		Numerical ratios of monoecious ( $AA + Aa$ ) : androecious ( $aa$ ) plants obtained on selfing (s)			Numerical ratio of monoecious ( $Aa$ ) : androecious ( $aa$ ) plants obtained on mating with androecious plants (c)		
symbol	expected genetic composition	actual	theoretical	P	actual	theoretical	P
D1	$Aa$	88 : 26	3 : 1	>0.50	46 : 41	1 : 1	>0.50
D2	$AA$	25 : 0			51 : 0		
D3	$AA$	122 : 0			117 : 0		
D4	$Aa$	92 : 37	3 : 1	>0.20	61 : 68	1 : 1	>0.50
D5	$AA$	73 : 0			40 : 0		
D6	$Aa$	19 : 6	3 : 1	>0.80	47 : 50	1 : 1	>0.50
D7	$Aa$	42 : 23	3 : 1	>0.05			
D8	$Aa$	158 : 47	3 : 1	>0.20	58 : 54	1 : 1	>0.50
D8(NAA)	$Aa$				26 : 21	1 : 1	>0.20
D9	$Aa$				62 : 67	1 : 1	>0.50
D10	$AA$	56 : 0			16 : 0		
D11	$Aa$	85 : 31	3 : 1	>0.50	52 : 44	1 : 1	>0.20
D12	$Aa$				34 : 41	1 : 1	>0.20
D13	$AA$	17 : 0			95 : 0		
D14	$AA$	99 : 0			79 : 0		
D2s	$AA$	25 : 0			111 : 0		
D2c	$Aa$	120 : 44	3 : 1	>0.50	79 : 72	1 : 1	>0.50
D4c	$Aa$	241 : 79	3 : 1	>0.80	67 : 54	1 : 1	>0.20
D8c	$Aa$				37 : 43	1 : 1	>0.50
D13c(NAA)	$Aa$				14 : 14	1 : 1	>1.00
Total		845 : 293	3 : 1	>0.50	583 : 569	1 : 1	>0.50

This way, each of the fourteen monoecious plants chosen afforded at least two fruits — one upon selfing and the other on mating with the androecious form. Seeds from these fruits were planted into the ground in springtime of 1967, and subjected to separate observations of sexuality in the different generations. In some cases, as e.g. in the D7, D9 and D12 plants, part of the fruits either remained seedless or produced barren seeds — hence the missing analyses of the respective generations.

In 1968, under similar conditions of cultivation, additional analyses were carried out on generations: D2s, D2c, D8c and D13c derived from the selfed (s) and crossed (c) generations observed in 1967.

Genetic composition of plants has been made out on grounds of the sexuality of the offspring, the quantitative ratio of mono- and androecious plants being compared with the theoretical ratios by means of the *Chi*-square criterion and the deviations observed being estimated by the probability rate P.

## RESULTS

Table 1 makes it clear that the trait of maleness in the tested plants is governed by a single recessive gene which has been given the denomination *a* (androecious).

Androecious plants have a composition *aa*, whereas monoecious plants — *AA* or *Aa*. Homozygous, monoecious plants *AA* do not differ in their external appearance from heterozygous forms *Aa* and thus are identifiable exclusively on the basis of sexuality of their offspring.

Progeny of the homozygous, monoecious plants is in all cases entirely monoecious, both on self-pollination and on pollination with the androecious plants; whereas the offspring of heterozygous plants segregates on self-fertilization into monoecious and androecious plants, 3 : 1 approximately, and on pollination by the androecious plants in a ratio of 1 : 1 in general. Differences between the obtained ratios and those calculated on grounds of the monogenic pattern of inheritance are insignificant; evidence lies in the high single and general probability values concerning the deviations observed.

All the monoecious plants of the examined generations exhibited similar sexuality independently from the genetic make-up. The first pistillate flowers on the main stems usually formed in these plants in the  $10.3\text{th} \pm 0.251$  node and the average ratio of staminate to pistillate flowers on the entire plant was  $0.6 \pm 0.16$  (Fig. 1). With this we have a rare case of monoecious plants in *Cucurbita*, which are characteristic of developing twice as many pistillate flowers, than of staminate flowers, under normal conditions of cultivation. According to the previous findings (Erwin and Haber, 1929; Whitaker, 1931; Wittwer and Hillyer, 1954; Hopp, 1962) monoecious plants manifested a much greater intensity of maleness.

It should be mentioned, nevertheless, that the ratio of staminate to pistillate flowers found in the tested monoecious flowers changes with their proceeding development. At first, during the earliest stages, plants bring out exclusively staminate flowers (Fig. 1 — apex designated by a broken line). Interestingly, earliest pistillate flowers on the main stems and on lateral shoots are formed more or less above the same number of nodes counting from the base. As soon as the first pistillate flowers come into existence on the main stems and lateral shoots their proportion starts to increase with the development of the plant at the expense of staminate flowers; yet under the cultivation applied, entire suppression of male-flower development does not occur.

Androecious plants produce exclusively staminate flowers throughout the whole growing season. At first these plants show no difference from the monoecious forms, distinctive features of a more lush growth appearing no sooner than at later stages. Towards the end of the season androe-

cious plants are capable of giving rise to a number of nodes twice that in monoecious plants which had produced fruits earlier. Possibly these dissimilarities are due to growth inhibition in monoecious plants caused by the developing fruits — evidence being derived from the fact that monoecious forms deprived at early stages of the primordia of fruits equal in growth rate the androecious plants.

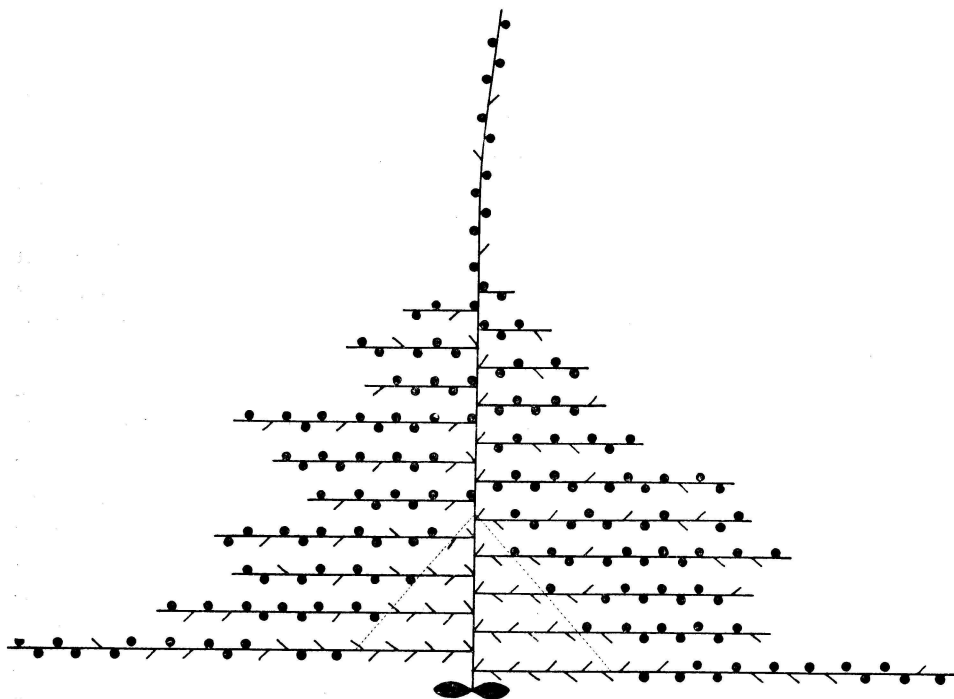


Fig. 1. Diagrammatic representation of a typical distribution of staminate (broken line) and pistillate (circles) flowers and the quantitative ratios in monoecious form of *Cucurbita pepo* var. Greckie

Making use of the known facts of pistillate-flower growth stimulation by auxins in cucurbits (Nitsch *et al.*, 1952; Wittwer and Hillyer, 1954) attempts have been undertaken to induce the development of pistillate flowers in androecious plants of androdioecious populations with the application of auxins. For this purpose part of the D8 generation and the whole D13c generation were sprayed twice over (the former in 1957 and the latter in 1968) with 1-naphthylacetic acid, 100 ppm.

In both cases the first spray took place at the first-leaf stage while the next one a week later. As shown in Table 1, these treatments failed to alter the ratio of androecious to monoecious plants. As in the untreated specimens, they remained at the 1:1 standard. In monoecious plants, too, of the treated populations, no marked changes were noticed beyond



a slightly earlier appearance of pistillate flowers. Though not all the opportunities of inducing the development of pistillate flowers in androecious plants have been put to use, it can be ascertained that maleness of these plants is a stable trait, fairly resistant to the influence of external factors.

## DISCUSSION

Androecious plants in *Cucurbita pepo* referred to in the present paper are similar in their genetic composition to androecious plants in *Cucumis sativus* (Kubicki, part VI, 1969). In both cases maleness is a recessive feature in respect to monoecism. Androecious plants in cucumber exhibit, however, a lesser stability. Unlike androecious plants in *Cucurbita pepo* they are capable of developing single pistillate flowers in response to some of the external factors. This shows that genes *a*, usually similar in their action, differ in these species in their ability to restrain the development of pistillate flowers, i.e. to check the synthesis of an ovary-forming substance.

There is still another case of similarity in the mechanism of staminate and pistillate flower differentiation in these species.

Galun and Atsmon (1960) as well as Atsmon and Galun (1962) have inferred that the genetic as well as environmental factors, both influence sex differentiation in that they alter the developmental stages of flower buds in respect to the adjoining leaves. Thus, genes which govern femaleness as well as short-day conditions and low temperatures have the same effect and cause hastening of development of flower buds resulting in their differentiation into pistillate flowers in the angles of younger leaves, and in their more advanced development in comparison with staminate flowers in the angles of similarly-aged leaves.

This phenomenon has proved much more notable in monoecious and androecious forms of *Cucurbita pepo* observed by the author (Fig. 2). In monoecious plants the pistillate flowers differentiate earlier in the contiguity of younger leaves and attain much more advanced developmental stages than staminate flowers which become formed in angles of leaves of the same age. In effect, pistillate flowers open into bloom several nodes earlier, on the same stem, than the staminate flowers.

As compared with leaves, staminate-flower initiation and growth rate in androecious is similar to that in monoecious plants (Fig. 2). It seems as if — in *Cucumis sativus* and *Cucurbita pepo* — there were an analogous mechanism of sex differentiation which regulates the interrelationships between the age of leaves and flower buds coming forth in their angles. In the androecious plants, genes *a* retard the differentiation of flower buds which occurs in the neighbourhood of older leaves. Possibly the more stable character of androecious plants in *Cucurbita pepo* is due to

higher, than in cucumber, age differences in leaves in the angles of which staminate and pistillate flowers come to be differentiated. This kind of differences present more difficulty in being abolished.



Fig. 2. Stems: left — monoecious; right — androecious. A comparative illustration of the rate of differentiation and of development of the pistillate and staminate flowers

Above described mechanism of sex differentiation based on the association between flower buds and the age of leaves seems to conform closely to the hormonal theory — evidence coming from experimental findings reported by Galun (1959) and by Galun *et al.* (1965). After this theory and in agreement with Vavilov's law of homologous series, as was the case with cucumbers, in *Cucurbita pepo* there may still occur other sex types, e.g. gynoeceous plants.

From the character of androecious plants in *Cucurbita pepo* it can be inferred that in case of obtaining gynoeceous plants the synthesis of dioecism in this species would be easier than in cucumber.

#### SUMMARY

Androecious plants obtained on selfing in *Cucurbita pepo* var. Greckie represent a new sex type. Differences in the sex character between monoecious and androecious plants are conditioned by a single pair of alleles

*Aa*. Monoecious plants have a composition *AA* or *Aa*, while androecious plants — *aa*.

Monoecious plants carrying one or two genes *A* do not differ from one another externally; under normal conditions of field cultivation they produce staminate and pistillate flowers in a 0.6 : 1 ratio, more or less. Androecious plants develop throughout the whole growing season exclusively staminate flowers, and even auxins fail to stimulate the appearance on pistillate flowers in these forms.

Pistillate flowers in monoecious plants come forth at an earlier period in angles of younger leaves and exhibit a much higher growth rate than staminate flowers in monoecious and androecious plants.

These data show the mechanism of sex determination in the studied variety of *Cucurbita pepo* to be similar to that in cucumber.

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#### Streszczenie

#### ROŚLINY MĘSKIE U *CUCURBITA PEPO* L.

Otrzymane w wyniku samozapylenia rośliny męskie u *Cucurbita pepo* odmiany Greckie stanowią nowy typ płciowy. Stwierdzono, że różnice w charakterze płciowym pomiędzy roślinami jednopiennymi i męskimi uwarunkowane są jedną parą alleli *Aa*. Rośliny jednopienne posiadają skład *AA* lub *Aa*, a męskie *aa*. Rośliny jednopienne z jednym i dwoma genami *A* nie różnią się pomiędzy sobą i w normalnych warunkach uprawy polowej wytwarzają kwiaty męskie i żeńskie przeciętnie w stosunku 0.6:1. Rośliny męskie wytwarzają przez cały okres wegetacji wyłącznie kwiaty męskie i nawet auksyny nie stymulują u nich rozwoju kwiatów żeńskich.

Stwierdzono, że kwiaty żeńskie u roślin jednopiennych różnicują się wcześniej w kątach młodszych liści i wykazują znacznie szybsze tempo rozwoju w porównaniu z kwiatami męskimi u roślin jednopiennych i męskich.

Dane te wskazują, że mechanizm determinacji płci u badanej odmiany *Cucurbita pepo* jest podobny jak u ogórków.