

# THE GENETICS OF SEX DETERMINATION IN THE FAMILY AMARANTHACEAE\*

MERRITT J. MURRAY  
*Cornell University, Ithaca, New York*<sup>1</sup>

Received March 18, 1940

## INTRODUCTION

AS HAS been emphasized by YAMPOLSKY (1922, 1925) angiospermous plants exhibit many physiological as well as morphological forms of sex expression. Many of these forms appear to be intermediate steps in the evolution of one type into that of another, as has been suggested by CORRENS (1928) and others. EMERSON (1924), JONES (1934), and LEBEDEFF (1938) have predicted that the many gene mutations which affect sex in maize are the building blocks that could lead to the development of a different type of sex expression in this plant. In fact, EMERSON (1932) and JONES (1932, 1934) have produced dioecious strains of maize by the proper combinations of two genes.

Is the evolution of dioecious forms from hermaphroditic ones, or the reverse, explainable on such a simple genetic basis? CORRENS (1907, 1928) early attempted to solve this question by direct hybridization, but the sterility of his F<sub>1</sub> hybrids did not allow him to continue his analysis beyond the first generation. Recent work on cultivated species and varieties indicates that sex expression is markedly influenced by a few gene mutants having very specific actions. STOREY (1938 a, b) and HOFMEYR (1938) believe that a single gene with two alleles will explain much of the sex variability within the species *Carica Papaya*. OBERLE (1938) found that variations in the sex expression of *Vitis* species, varieties, and hybrids is best explained on the basis of two allelic pairs of factors which are completely linked. ROSA (1928) has shown that a monoecious condition in muskmelons is dominant to an andromonoecious condition and that this difference is due to a single factor. POOLE and GRIMBALL (1939) have shown that monoecious and perfect-flowered varieties of muskmelons differ in two gene mutations and that the perfect-flowered form is genetically the double recessive type. Do these same conclusions apply to natural species which have evolved two different but stable sex forms?

The work reported in this paper represents a search for suitable material which would allow a direct genetic analysis of second generation progeny

\* The cost of the accompanying half tone illustrations has been borne by the Galton and Mendel Memorial Fund.

<sup>1</sup> Paper No. 231, Department of Plant Breeding, Cornell University, Ithaca, New York. Based on a thesis presented to the Faculty of the Graduate School of Cornell University for the degree Doctor of Philosophy.

resulting from the hybridization of dioecious and hermaphroditic forms. Members of the family Amaranthaceae were selected at PROFESSOR R. A. EMERSON'S suggestion, since he had observed in nature sterile  $F_1$  hybrids arising from the natural hybridization of a monoecious and a dioecious species. As a large number of closely related monoecious and dioecious species are available in this group of plants, certain combinations might be found which would give fertile hybrids, unless there is some direct relation between sterility and the evolution of sex differences. A detailed account of this work is given here. Preliminary reports in abstract form have already been published (MURRAY 1938, 1939, 1940 a, b).

## MATERIALS AND METHODS

Species which have been used successfully in crosses are given in table 1. Numerous pollinations were also made between this material and species in other genera such as *Celosia*, *Gomphrena* and *Achyranthes* but no hybrids were obtained.

TABLE I  
*Origin, sex, and chromosome number of the species used in this study.*

SPECIES	ORIGIN	SEX	N CHROMOSOME NUMBER
<i>Amaranthus hybridus</i> L. Angol race	Near Angol, Chile	Monoecious type 1	16
<i>Amaranthus hybridus</i> Line 58	Ithaca, N. Y.	Monoecious type 1	16
<i>Amaranthus hybridus</i> Line 56	Ithaca, N. Y.	Monoecious type 1	16
<i>Amaranthus caudatus</i> L. var. leucospermus (Wats.) Thell. Mexican race	Mexico	Monoecious type 1	16
<i>Amaranthus caudatus</i> L. var. leucospermus (Wats.) Thell. Manchurian race	Manchuria	Monoecious type 1	16
<i>Amaranthus retroflexus</i> L.	Ithaca, N. Y.	Monoecious type 1	17
<i>Amaranthus Powellii</i> Wats.	Kansas Ithaca, N. Y.	Monoecious type 1	?
<i>Amaranthus spinosus</i> L.	Central Yucatan Belle Glade, Fla.	Monoecious type 2	17
<i>Acnida tamariscina</i> (Nutt.) Wood	Lincoln, Neb.	Dioecious	16
<i>Acnida cuspidata</i> Bert.	Canal Point, Fla.	Dioecious	16
<i>Acnida tuberculata</i> Moq.	Westerville, Ohio	Dioecious	16

The material was identified by DR. P. C. STANDLEY of the Field Museum of Natural History who has monographed this family. It is well known by taxonomists that this is, at least in part, a difficult group and that the correct application of names in some cases requires study of type specimens present in European herbaria. To know the exact material used in this study, reference may be made to specimens deposited in the Cornell University herbarium or the Field Museum of Natural History, Chicago.

The three races of *Amaranthus hybridus* have been treated as though they were species since they are morphologically distinct in habit, leaves and inflorescence characters. They breed true to type and at least part of their hybrid combinations are almost completely sterile.

While taxonomic manuals disagree in their descriptions of the sex of the several members of the genus *Amaranthus*, the races and species which I have used are strictly monoecious. The arrangement of the staminate and pistillate flowers within the inflorescence is a very definite one. This may be seen from a consideration of the growth pattern shown by the species used in this work. The main axis of the inflorescence is usually branched.

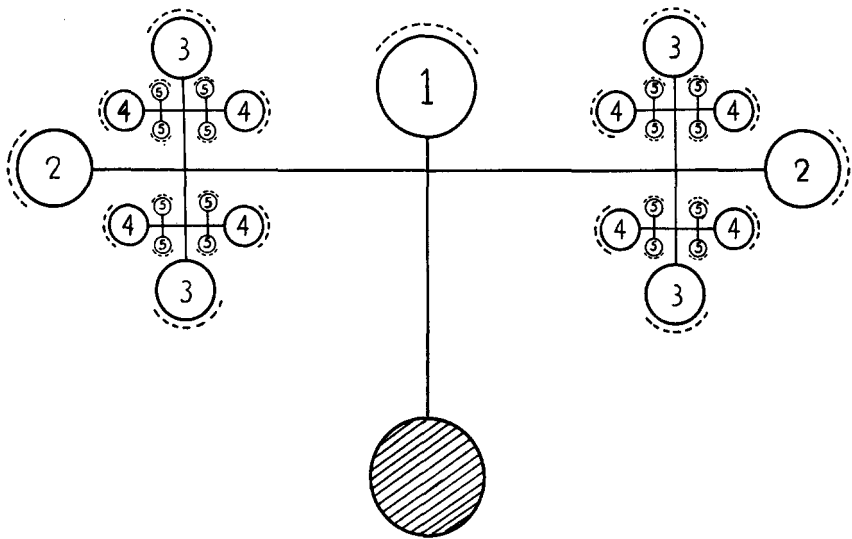


FIGURE 1.—Diagrammatic illustration of the arrangement and development of individual flowers within a flower cluster. A broken line indicates the position of the bract which subtends each flower. The shaded circle is the main axis of the inflorescence.

The length and number of these branches and their angle with the main axis determine the shape of the inflorescence. Individual flower clusters develop along these axes in an alternate fashion, while within each flower cluster, individual flowers are produced as illustrated diagrammatically in figure 1. The first flower is terminal on the branch and at its base, two branches develop the second and third flowers. Each of these flowers in turn is terminal and at its base develop the next two flowers. This process continues until all the available space is occupied. Development is usually very symmetrical up to the third or fourth series of flowers. At this time the setting of the first seed usually slows down growth and upsets the symmetry. Unpollinated clusters may develop as many as 250 flowers. My diagram has purposely exaggerated distances between the flowers and has also

placed the branches exactly opposite each other as they appear to be in gross dissections. The apparently opposite branching in the flower cluster is probably produced by shortening the axes of an alternate branching system.

This growth pattern is common to all the species regardless of sex. In the dioecious species, the flower clusters not only have all their flowers of the same sex but all the flower clusters on one plant are of the same sex. The monoecious species exhibit two types of arrangement of the staminate and pistillate flowers. These types are important because of their different breeding behavior.

In the first type, the first flower of each flower cluster is staminate and all the succeeding ones are pistillate. There is only one staminate flower in each flower cluster of the inflorescence and this abscises soon after shedding pollen. The monoecious species of *Amaranthus* except *Amaranthus spinosus* belong to this group.

In the second type, all the flowers of each cluster are of the same sex but the clusters of pistillate flowers develop only in the axils of the branches and at the base of the terminal inflorescence while the clusters of staminate flowers are borne terminally on the main axis and lateral branches. *Amaranthus spinosus* is of this type.

All species used in this study are wind-pollinated. The monoecious members are chiefly self-pollinated, although the stigmas of the pistillate flowers are receptive several days prior to the opening of any staminate flowers. The small, closely grouped flowers of the monoecious species made emasculation extremely difficult. The most satisfactory method of making crosses onto the monoecious species is to pollinate heavily as soon as the stigmas are receptive and to remove the staminate flowers by hand. Even so, 5-25 percent self-pollination usually occurs. The hybrids are easily distinguished from the monoecious parent and in several crosses dominant genes have been used to distinguish the hybrids in the seedling stage.

Six kinds of crosses have been made and will be discussed in the order given below.

1. Interspecific crosses of dioecious species of *Acnida*.
2. Interspecific crosses of monoecious species of *Amaranthus*.
3. Intergeneric crosses of dioecious species of *Acnida* and monoecious "first type" species of *Amaranthus*.
4. Intergeneric crosses of dioecious species of *Acnida* and monoecious "second type" species of *Amaranthus*.
5. Backcross of  $F_1$  hybrids obtained from "3" to both parental types.
6. Backcross of  $F_1$  colchicine-induced tetraploid hybrids obtained from "3" to both parental types.

## RESULTS

*Interspecific crosses of dioecious species of Acnida*

Three different dioecious species breed true to type and give normal 1:1 sex ratios (table 2). All six possible  $F_1$  hybrids have been made and each of these gives a 1:1 sex ratio, with the possible exception of the first cross which shows a deviation slightly greater than should be expected by chance.

TABLE 2

*Hybridization results of interspecific crosses of dioecious species of Acnida.*

CROSS	FEMALE	MALE	D./P.E.	
			1:1	1:2
A. Control—Dioecious species inbred:				
<i>Acnida tamariscina</i> (Nutt.) Wood	2259	2291	.75	
<i>Acnida cuspidata</i> Bert.	72	64	1.02	
<i>Acnida tuberculata</i> Moq.	43	39	.66	
B. First generation progeny of interspecific crosses:				
<i>A. tamariscina</i> × <i>A. cuspidata</i>	752	664	3.47	
Reciprocal	622	568	2.32	
<i>A. tamariscina</i> × <i>A. tuberculata</i>	83	100	1.97	
Reciprocal	58	62	.54	
<i>A. cuspidata</i> × <i>A. tuberculata</i>	173	179	.47	
Reciprocal	80	102	2.42	
C. Second generation progeny of interspecific crosses:				
$F_2$ ( <i>A. tamariscina</i> × <i>A. cuspidata</i> )	196	167	2.3	
B.C. ( <i>A. tamariscina</i> × <i>A. cuspidata</i> ) × <i>A. tamariscina</i>	67	137		.22
$F_2$ ( <i>A. cuspidata</i> × <i>A. tamariscina</i> )	73	79	.72	
B.C. ( <i>A. cuspidata</i> × <i>A. tamariscina</i> ) × <i>A. tamariscina</i>	71	84	1.66	
B.C. ( <i>A. cuspidata</i> × <i>A. tamariscina</i> ) × <i>A. tamariscina</i>	49	116		1.46

The second generation progeny consist of normal male and female plants. Certain crosses give 1:1 sex ratios while other crosses give ratios of one female to two males. The latter type of cross is due apparently to the presence of a recessive sex-linked lethal carried in the X chromosome. If this is true, the genotypes of the  $F_1$  parents are  $X^1X^+$  and  $X^1Y^+$ . The male is known to be the heterogametic sex from genetic evidence presented later in this paper.

No intersexes, hermaphroditic plants, or sex abnormalities were found in the second generation progeny obtained from reciprocal hybridization of these two different dioecious species. Why should this be true? If individual chromosomes of these two species carry different quantitative amounts of

male and female determining factors (due either to the quantitative nature of a few genes or to the number of these genes), why does not the normal distribution of the chromosomes in the  $F_1$  hybrids result in the production of plants with an abnormal balance of sex factors? The segregation of two monofactorial differences furnishes genetic evidence that at least one or two chromosomes segregate in a normal manner and there is no evidence suggesting that other members behave differently. Two hypotheses to explain the above data are cited.

First, if sex is determined by a balance between many sex determiners which act in either a male or a female direction, we must almost certainly conclude that these two species have, chromosome for chromosome, an identical balance of these factors. This assumption seems unreasonable from an evolutionary viewpoint. Two species which differ primarily in quantitative characters probably have had genic changes in every chromosome (MURRAY 1940a). Major changes in the chromosome arrangement of the genic material have apparently occurred. Why should genes affecting size and shape of morphological structures mutate while genes influencing sex do not? If a primitive dioecious *Acnida* plant came originally from a hermaphroditic ancestor, we could postulate a mass mutation phenomenon to account for this fact. The further assumption follows that once this balance of many factors is created, stability of all or most of the sex factors results, even though mutation of other types continues. The dioecious and monoecious species of this group of plants are certainly closely related; otherwise one could hardly account for the 33 different intergeneric hybrids that have been obtained. The explanation just attempted becomes very complicated and may be disregarded as a much simpler hypothesis can explain the same data.

A few gene mutations of a very specific nature could occur and cause the evolution of a dioecious form from a hermaphroditic one. EMERSON (1932) and JONES (1932, 1934) have shown that this can be accomplished experimentally in maize, using only two mutants which have occurred spontaneously. Their examples have one mutant gene homozygous in both sexes; the second gene is homozygous in one sex and heterozygous in the other. These two factors are located on different chromosomes. The first gene may be termed an autosomal factor; the second gene creates the XX and XY mechanism. If all monoecious maize were suddenly exterminated and these dioecious races were saved, one would not be able to detect the presence of the autosomal gene. One might discover that one sex was homogametic and the other heterogametic.

The same reasoning may be applied to the sex mechanism in *Acnida* species. The autosomes either carry no genes influencing sex or carry them in a homozygous condition. If autosomal sex genes are present, they are prob-

ably few in number, since two dioecious species do not differ in this regard although they exhibit other major changes of chromosome structure and genic content. This discussion is concerned only with those factors which differentiate between hermaphroditic species and closely related dioecious species. There is abundant evidence in plants and animals that many loci on most or all of the chromosomes are concerned with the physiology and morphology of reproductive structures, but only those genes which are different in the two sex forms need enter into this discussion.

SCHAFFNER (1923) observed *Acnida tamariscina* and found that the sexual states of this species were extremely stable. I, too, have found that this species exhibits very few sex abnormalities, even under the extreme conditions of low light intensity and low temperature. Occasionally a staminate plant will produce a few flowers having a partially developed ovary. These more or less perfect flowers do not produce seeds as they wither and abscise soon after the pollen is shed. No abnormalities have been observed on pistillate plants.

Although the reversion of 101 females and 243 males to the vegetative state was observed, only one example of complete sex reversal has been found. This plant originally had about 25 male flowers. After growing vegetatively, the plant was entirely female and normal in every respect. Crosses made with this plant as a female gave 400 ♀ : 385 ♂ which shows that the plant had a female genotype even though a few male flowers were produced at one time.

#### *Interspecific crosses of monoecious species of Amaranthus*

All monoecious species and races breed true and have been inbred one to three generations before being used in crosses. The two types of arrangement of the staminate and pistillate flowers found in these monoecious species (table 1) are phenotypically very stable. Abnormalities are rarely encountered.

Thirteen crosses have been made between members possessing the first type of sex arrangement (table 3) and the hybrids, thus obtained, have the same sex arrangement. This result would be expected if all these species are homozygous for the factors controlling this particular positional placement of the staminate and pistillate flowers. These species hybridize readily but the  $F_1$  hybrids are so highly sterile that  $F_2$  plants are seldom obtained. The few that were secured did not show segregation. On the other hand, the high sterility makes it easy to get amphidiploid progeny following colchicine treatment of the growing point. When the treatment is effective, an abundance of seed is produced; otherwise, only a few seeds would be procured from an entire inflorescence. The five amphidiploids have the same sex arrangement as their parents.

TABLE 3

*Hybridization results of interspecific crosses of monoecious species of Amaranthus.*

CROSS OR SELF	MONOECIOUS	REMARKS
A. Control—Monoecious <i>Amaranthus</i> species selfed	Breed true to type	
B. Interspecific crosses of monoecious species:	(Number of plants)	
First type×first type:		
<i>A. hybridus</i> Angol race× <i>A. caudatus</i> Manchurian race	548	1st type
Reciprocal	119	1st type
<i>A. hybridus</i> Angol race× <i>A. caudatus</i> Mexican race	28	1st type
<i>A. hybridus</i> Angol race× <i>A. hybridus</i> Line 58	166	1st type
<i>A. hybridus</i> Angol race× <i>A. hybridus</i> Line 56	169	1st type
Reciprocal	71	1st type
<i>A. hybridus</i> Angol race× <i>A. Powellii</i>	124	1st type
<i>A. hybridus</i> Angol race× <i>A. retroflexus</i>	434	1st type
Reciprocal	363	1st type
<i>A. hybridus</i> Line 56× <i>A. Powellii</i>	1	1st type
Reciprocal	1	1st type
<i>A. hybridus</i> Line 58× <i>A. Powellii</i>	5	1st type
Reciprocal	15	1st type
<i>A. hybridus</i> Line 58× <i>A. retroflexus</i>	1	1st type
<i>A. retroflexus</i> × <i>A. Powellii</i>	9	1st type
Reciprocal	1	1st type
<i>A. caudatus</i> Mexican race× <i>A. retroflexus</i>	115	1st type
Reciprocal	5	1st type
<i>A. caudatus</i> Mexican race× <i>A. Powellii</i>	61	1st type
<i>A. caudatus</i> Manchurian race× <i>A. hybridus</i> Line 58	172	1st type
First type×second type:		
<i>A. caudatus</i> Manchurian race× <i>A. spinosus</i>	2	1st type
<i>A. retroflexus</i> × <i>A. spinosus</i>	2	1st type
<i>A. hybridus</i> Angol race× <i>A. spinosus</i>	20	Intermediate
C. F <sub>2</sub> progeny of interspecific crosses of monoecious species:		
F <sub>2</sub> ( <i>A. retroflexus</i> × <i>A. caudatus</i> Mexican race)	3	1st type
F <sub>2</sub> ( <i>A. retroflexus</i> × <i>A. spinosus</i> )	10	2nd type
D. Amphidiploid progeny of interspecific crosses of monoecious species:		
F <sub>2</sub> ( <i>A. hybridus</i> Angol race× <i>A. retroflexus</i> )	71	1st type
F <sub>2</sub> ( <i>A. caudatus</i> Mexican race× <i>A. retroflexus</i> )	106	1st type
F <sub>2</sub> ( <i>A. caudatus</i> Manchurian race× <i>A. hybridus</i> Line 58)	242	1st type
F <sub>2</sub> ( <i>A. caudatus</i> Manchurian race× <i>A. hybridus</i> Angol race)	49	1st type
F <sub>2</sub> ( <i>A. hybridus</i> Angol race× <i>A. hybridus</i> Line 58)	16	1st type

Members of the two types of sex arrangement hybridize with great difficulty. The plants that have been obtained are certainly hybrids as they show two dominant leaf color genes carried by the male parent. The first type is completely epistatic to the second type when the species *A. caudatus* and *A. retroflexus* are crossed to *A. spinosus*. An intermediate condition



TABLE 4

*F*<sub>1</sub> hybridization results of intergeneric crosses of dioecious species of *Acnida* and monoecious "first type" species of *Amaranthus*.

CROSS	♀ ♀	♂ ♂	D./P.E. 1:1
<i>Acnida cuspidata</i> × <i>Amaranthus retroflexus</i>	8	0	
Reciprocal	287	282	0.37
<i>A. cuspidata</i> × <i>A. hybridus</i> Angol race	717	0	
Reciprocal	453	411	2.31
<i>A. cuspidata</i> × <i>A. hybridus</i> Line 58	53	0	
Reciprocal	133	113	1.89
<i>A. cuspidata</i> × <i>A. caudatus</i> Mexican race	124	0	
Reciprocal	53	48	0.89
<i>A. cuspidata</i> × <i>A. caudatus</i> Manchurian race	73	0	
Reciprocal	144	121	2.19
<i>A. cuspidata</i> × <i>A. Powellii</i>	40	0	
Reciprocal	—*	—	
<i>Acnida tuberculata</i> × <i>Amaranthus retroflexus</i>	—	—	
Reciprocal	82	92	1.12
<i>A. tuberculata</i> × <i>A. hybridus</i> Angol race	346	0	
Reciprocal	276	314	2.32
<i>A. tuberculata</i> × <i>A. hybridus</i> Line 58	—	—	
Reciprocal	87	98	1.31
<i>A. tuberculata</i> × <i>A. caudatus</i> Mexican race	—	—	
Reciprocal	42	52	1.53
<i>Acnida tamariscina</i> × <i>Amaranthus retroflexus</i>	547	0	
Reciprocal	339	374	2.00
<i>A. tamariscina</i> × <i>A. hybridus</i> Angol race	1070	0	
Reciprocal	1536	2007	11.72
<i>A. tamariscina</i> × <i>A. hybridus</i> Line 58	251	0	
Reciprocal	191	173	1.40
<i>A. tamariscina</i> × <i>A. hybridus</i> Line 56	4	0	
Reciprocal	4	3	1.12
<i>A. tamariscina</i> × <i>A. caudatus</i> Mexican race	728	0	
Reciprocal	517	410	5.26
<i>A. tamariscina</i> × <i>A. caudatus</i> Manchurian race	805	0	
Reciprocal	315	429	6.20
<i>A. tamariscina</i> × <i>A. Powellii</i>	17	0	
Reciprocal	—	—	

\* Hybrids not studied; but readily obtainable.

results when *A. hybridus* is crossed to *A. spinosus*. These hybrids also have normal flowers but the staminate and pistillate flowers bear no precise positional arrangement with reference to each other. This condition is apparently related to certain factors present in the *A. hybridus* genom which interact only with certain factors in the genom of *A. spinosus* since *F*<sub>1</sub> hybrids between *caudatus*, *retroflexus*, and *hybridus* show no peculiarities.

*Intergeneric crosses of dioecious species of Acnida and monoecious  
"first type" species of Amaranthus*

The results obtained from reciprocal crosses between three different dioecious species and several monoecious first type species are summarized in table 4. All 29 of these intergeneric crosses are consistent in showing that dioeciousness is epistatic over monoeciousness. Fourteen of these crosses were made using the dioecious species as the female parent and these crosses give all female hybrids. The reciprocal crosses, where the monoecious species is the female parent, give ratios of approximately 1 ♀ : 1 ♂. These results are in agreement with CORRENS' (1907) work on *Bryonia*. His interpretation that the male is the heterogametic sex is likewise true for the three species of *Acnida*.

All crosses which involve the dioecious species *Acnida cuspidata* and *Acnida tuberculata* give progenies consisting exclusively of normal female hybrids and the reciprocal crosses give 1:1 sex ratios well within the expected deviations. This is not true of certain crosses with *Acnida tamariscina*. The summarized ratios, from certain of those crosses which segregate for males and females, exhibit deviations from a 1:1 ratio much greater than would be expected by chance. Many of the hybrids do not produce flowers and thus there is omitted from table 4 a considerable number of plants whose sex could not be determined. An analysis of individual crosses with consideration given to the non-flowering plants is necessary for an understanding of this problem.

*Neuter plants.* Plants which do not bear flowers will be designated in this paper as neuter plants. They are indistinguishable from normals in so far as the vegetative parts of a plant are concerned. Neuter plants develop an inflorescence devoid of the actual flowers. The bracts which subtend normal flowers are present but not even minute rudiments are externally visible to indicate that the flower primordium began development. Presumably because the flowers are not present to make nutritional demands on the plant, the individual axes within each flower cluster continue to grow rapidly and a large, crowded, bract-filled inflorescence results. The only fundamental difference is the absence of flowers, as the growth pattern is unchanged.

Neuter plants occur only in the hybrids arising from crosses of the dioecious species *Acnida tamariscina* to any of the monoecious first type species. It must be emphasized that the monoecious species which are used in these crosses are normal in appearance and had been inbred one to three generations. Likewise, *Acnida tamariscina* progeny were grown in considerable numbers without finding any sexual abnormalities and all crosses were made on plants which were inbred one or two generations. It was thought (MURRAY 1938) that the neuter plants were due to an environmental effect on an unstable hybrid complement. An analysis of a larger number of

crosses now shows that the type of segregation depends on the particular *Acnida* male or female plant used in the cross. Individual plants of either sex give hybrid progenies with no neuter plants, fifty percent neuter plants, or all neuter plants (table 5).

TABLE 5

*Types of segregation for neuter plants in reciprocal crosses of Acnida tamariscina to the monoecious "first type" species.*

<i>Acnida tamariscina</i>	NUMBER OF PLANTS IDENTIFIED	F <sub>1</sub> PROGENY			D/PE 1:1	χ <sup>2</sup> 1:1:2
		♀ ♀	♂ ♂	NEUTER		
As female parent:						
Free from neuter	10	1923	0	6*		
Heterozygous for neuter	12	1255	0	1230	.74	
Homozygous for neuter	4	4*	0	292		
As male parent:						
Free from neuter	2	406	510	0	5.09	
Heterozygous for neuter	9	1316	1499	2035	5.09	138.9
Homozygous for neuter	1	1*	0	462		

\* Presumably off-pollinations or mechanical mixture of seeds.

The original race of *A. tamariscina* obtained from nature must have been heterozygous for a single dominant factor which induces neuterness when outcrossed to any of the monoecious species. Differences, even in chromosome number, between the monoecious species have no effect on the segregation of neuter in the resulting hybrids. Proof of this comes from the fact that at least three monoecious species with differences in chromosome numbers have been crossed to the same *Acnida* male or female plant in each of the six classes of segregations found in table 5.

There is a considerable deficiency in the number of neuter progeny in the cross of monoecious by heterozygous male, as one should expect a ratio of 1 ♀ : 1 ♂ : 2 neuter assuming that the factor is independent of sex. This deficiency is probably not to be ascribed to a lower viability of the neuter plants since in the reciprocal cross the neuter progeny appear with the expected frequency. In these same crosses the frequency of the males is out of proportion to that of the females, although not more so than in the cross where neuters are not present. The neuter-inducing factor inhibits the development of flowers of both sexes although not always in equal proportions. These discrepancies are even greater when one considers the results from any one male plant. The variability encountered includes such extreme ratios as 62 ♀ ♀ : 331 ♂ ♂ : 310 neuter and 424 ♀ ♀ : 307 ♂ ♂ : 548 neuter. A ratio of 271 ♀ ♀ : 278 ♂ ♂ : 408 neuter is much more nearly that expected if there is no linkage with sex. Pollen grains carrying the neuter

factor appear not to function as frequently as those carrying the recessive allele. No satisfactory explanation of these deviations is possible at the present time.

If a female plant of *Acnida tamariscina* known to be free of the neuter factor is crossed to an *A. tamariscina* male known to be heterozygous for the factor, the F<sub>1</sub> male plants segregate for bad pollen. Twelve plants had good pollen and eleven had about 50 percent pollen abortion. Likewise, if a female plant known to be homozygous for the neuter factor is crossed to a male plant known to be heterozygous, the F<sub>1</sub> males segregate. Twenty-seven F<sub>1</sub> plants had good pollen and 12 plants had about 50 percent pollen abortion. These records indicate that the neuter-inducing factor when heterozygous is associated with 50 percent pollen abortion and probably with 50 percent ovule sterility. A cytological study has not yet been made to ascertain whether a chromosomal change is actually present.

*Flower color.* The species *Acnida tamariscina* exhibits variations in plant color and an attempt was made to study these in the hope of obtaining a sex-linked character. Crosses of entirely green-stemmed plants to brilliant red-stemmed ones gave apparently heterozygous intermediate red-stemmed plants. When one of these heterozygous females is crossed to a monoecious species, linkage with the neuter-inducing factor is found. The results are given in tabular form below:

Red ♀	Green ♀	Red neuter	Green neuter
1	322	344	4
182	5	4	153

Since these are essentially backcross progenies, the two linkage phases may be added together in the calculation of the percent of recombination (1.4 percent).

The results of a second generation analysis of plant color in the species *Acnida tamariscina* are difficult to interpret. They suggest that the interaction of two autosomal genes are responsible for the type of plant color. It has been shown that one of these genes is closely linked to the neuter-inducing factor and that the latter is probably related to a chromosomal change. While an unknown translocation or inversion by itself ought not to disturb the ratios, partial linkage with a lethal would. This seems to be true. The neuter factor may be considered an autosomal factor since the closely linked color factor does not show sex linkage.

Neuter hybrids occasionally have small chimeras in the inflorescence and these areas bear either normal staminate or pistillate flowers. In those families where the neuter hybrids are all modified females these chimeras have pistillate flowers. In other families, where the neuter hybrids may be either modified males or females, some of the plants have pistillate

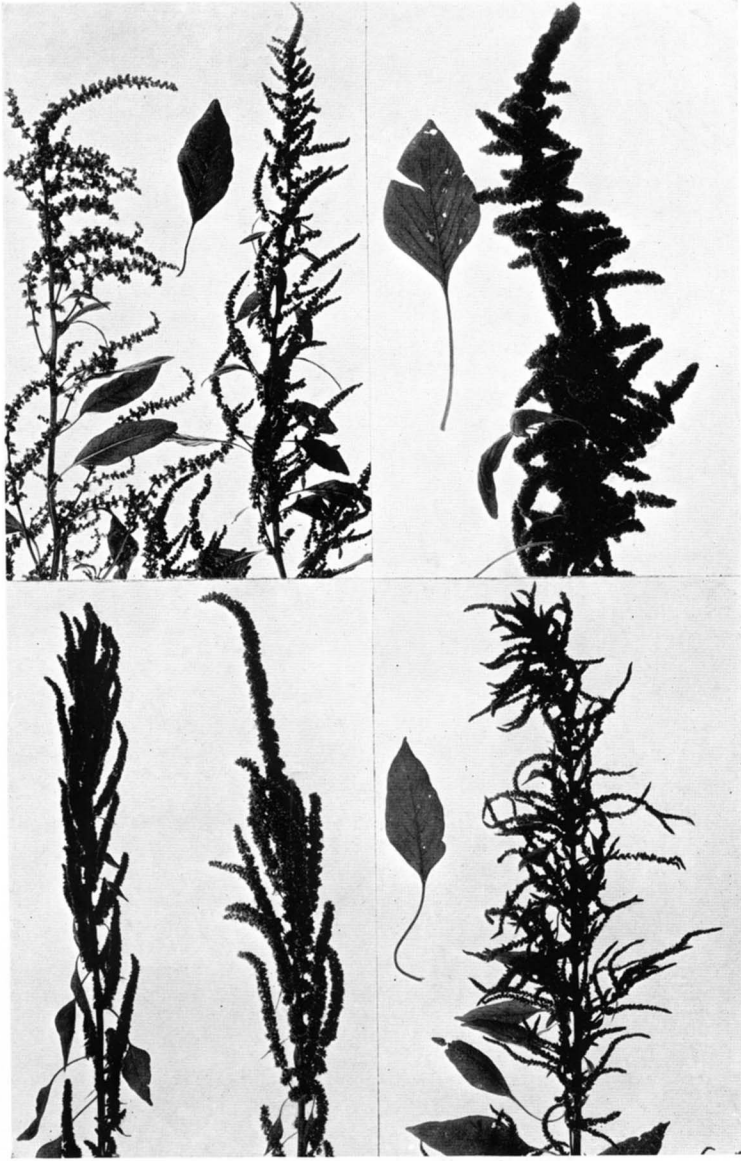


FIGURE 2. a (upper left).—Normal *Acnida tamariscina* (dioecious). Male at left, female at right. b (upper right).—*Amaranthus hybridus* Angol race, a monoecious first type species. c (lower left).—F<sub>1</sub> female (left) and male (right) hybrids resulting from the cross of *Amaranthus hybridus* Angol race by *Acnida tamariscina* male. d (lower right).—F<sub>1</sub> neuter hybrid resulting from the same cross.



FIGURE 3. a (upper left).—F<sub>1</sub> neuter hybrid resulting from the cross of *Amaranthus hybridus* Angol race by *Acnida tamariscina* male. Arrow points to chimera of normal male flowers. b (upper right).—Viable F<sub>1</sub> male hybrid resulting from cross of *Acnida tamariscina* by *Amaranthus spinosus*. Picture includes only one branch of a plant five feet tall. c (center).—Barely viable F<sub>1</sub> male hybrid resulting from the same cross. Note the size of this complete plant (1¼ inches tall) of approximately the same age as the plant figured in b. d (lower left).—*Amaranthus spinosus*, a monoecious second type species. Arrow indicates division line between female (below) and male flower clusters (above). Note lighter V-shaped area on leaf due to presence of a dominant gene. e (lower right).—F<sub>1</sub> monoecious hybrid resulting from cross of *Amaranthus hybridus* Angol race by *Amaranthus spinosus*. No definite positional arrangement of the staminate and pistillate flowers.

chimeras, others staminate ones. The sex of the  $F_1$  hybrids is quite stable in that staminate and pistillate flowers are rarely found on the same plant. The only observed exceptions were a few neuter plants which had both staminate and pistillate chimeras. Figure 3a illustrates a striking example of a large chimera where normal male development occurs on one side of a neuter plant. A cytological study of the male flowers of this chimera showed that development was halted before division I. It was therefore impossible to learn whether one or more chromosomes had been lost somatically.

One family not included in table 4 or 5 was a cross of *Acnida tamariscina* by *Amaranthus hybridus* Angol race. This cross gave 3 female to 11 monoecious plants. The flower arrangement of the monoecious hybrids was identical to that of the monoecious parent and somatic chromosome counts on one monoecious hybrid did not reveal any deviation from the expected number of 32 chromosomes. Apparently the particular *Acnida* female used in the cross was heterozygous for a mutation affecting sex, but unfortunately no other crosses were made on the same plant and this type of cross has not reappeared. Since part of these plants were grown in the greenhouse and part in the experimental plot, it is unlikely that this change was due solely to environmental causes. All the hybrid plants were pollinated but produced no fertile seed.

BRESSMAN (1934) has noted a high percentage of non-flowering (neuter) hop plants in certain cultures. Whether there is any real similarity between the neuter plants found in *Acnida* and hops cannot be determined from the published facts.

*Intergeneric crosses of dioecious species of Acnida and  
monoecious "second type" species of Amaranthus*

*Amaranthus spinosus* does not hybridize as readily with the dioecious species as do the monoecious first type species. The first progenies of these hybrids consisted entirely of small plants which usually died in the seedling stage. The fourth cross in table 6 is an example. Twenty-two plants out of 350 survived until they flowered and these grew very slowly for five months and never attained a height of more than two inches. This non-viability is associated with certain crosses and not with others. The first three families (table 6) indicate that progenies may be obtained consisting of all non-viable seedlings, 50 percent non-viable seedlings, or all viable seedlings. The dominant factor responsible for non-viability in the hybrids is probably carried in the dioecious species, *Acnida tamariscina*, since the *Amaranthus spinosus* plants came from a line inbred for two generations. In fact, this non-viability factor may be identical with the factor which induces the development of neuter hybrids in crosses with the monoecious first type species.

Disregarding non-viable progeny, males predominate in the cross dioecious by monoecious where all females would be expected if the monoecious parent had been one of the first type species. In addition to the males a limited number of monoecious plants are produced. In the reciprocal cross, males also predominate. Apparently male-determining factors present in the monoecious genom are epistatic over female-determining factors present in the dioecious genom.

TABLE 6

*F*<sub>1</sub> hybridization results of intergeneric crosses of dioecious *Acnida* species and *Amaranthus spinosus*, the monoecious "second type" species.

CROSS	♀ ♀	♂ ♂	MONOE- CIOUS	REMARKS
<i>Acnida tamariscina</i> × <i>Amaranthus spinosus</i>	0	347	3	No loss of seedlings
<i>Acnida tamariscina</i> × <i>Amaranthus spinosus</i>	6	207	41	50% loss of seedlings
<i>Acnida tamariscina</i> × <i>Amaranthus spinosus</i>	0	3	0	± 100% loss of seedlings
<i>Amaranthus spinosus</i> × <i>Acnida tamariscina</i>	1	17	4	All are type usually dying as seedlings
<i>Amaranthus spinosus</i> × <i>Acnida tamariscina</i>	0	186	4	No loss
<i>Amaranthus spinosus</i> × <i>Acnida cuspidata</i>	0	3	3	No loss
<i>Amaranthus spinosus</i> × <i>Acnida tuberculata</i>	0	52	7	No loss

It is difficult to know how much significance should be attached to the occurrence of the monoecious plants enumerated in table 6. Pistillate flowers are developed sporadically in the lowermost axils of these plants and vary in number from a few flowers to a maximum not exceeding 5 percent of the total. While a hybrid with 10,000 staminate flowers and only 25 pistillate flowers may be called monoecious, it is not strictly comparable to its monoecious parent which has an equal number of staminate and pistillate flowers. A study of phenotypic expression gives one the impression that factors which localize the development of the staminate flowers at the ends of the inflorescence branches in *A. spinosus* are lax in their effects in the hybrids and allow the production of staminate flowers throughout the plant with the possible exception of the lowermost axils which ordinarily do not produce flowers. Stem cuttings taken from the base of a hybrid plant, sometimes at least, produce an abundance of female flowers. The few female plants are most difficult to explain on a genotypic basis. Furthermore, the three monoecious hybrids found in the cross of *Amaranthus spinosus* by *Acnida cuspidata* approach the normal monoecious parent much more closely in phenotypic expression. One of these plants was a tetraploid.

*Backcross of F*<sub>1</sub> hybrids obtained from "3" to both parental types

The primary aim of this work was to find a hybrid combination of stable dioecious and monoecious species which would be fertile enough to enable



one to study backcross progenies. The dioecious species of *Acnida* have a haploid chromosome number of 16, the monoecious species of *Amaranthus* 16 or 17. This indicates that *Amaranthus hybridus* and *caudatus* are more closely related to *Acnida* than are *retroflexus* or *spinosus*. Yet all cross readily with *Acnida* to give F<sub>1</sub> hybrids. All F<sub>1</sub> hybrid combinations exhibit about 99 percent pollen abortion and the ovule sterility must be equally as great, although this is more difficult to estimate. A cytological examination of the microsporocytes of one intergeneric hybrid showed that chromosome distribution in the first division is very unequal and is even more unequal in the second division. This fact by itself could account for the high sterility. It is interesting that fertility in the hybrids is restored concurrently with the doubling of the chromosome complement. This indicates that failure to synapse properly is probably the major cause of this sterility.

TABLE 7

*Backcross of F<sub>1</sub> hybrid females (derived from intergeneric crosses) to parental types.*

CROSS	♀	♂	NEUTER	MONOECIOUS		D/PE 1:1
				NOR- MAL	SPO- RADIC	
Plot E and F. Backcross to dioecious parent						
F <sub>1</sub> ( <i>Acnida tamariscina</i> × <i>Amaranthus hybridus</i> Angol race) × <i>A. tamariscina</i>	488	520	15	0	6	1.50
F <sub>1</sub> ( <i>Acnida tamariscina</i> × <i>Amaranthus retroflexus</i> ) × <i>A. tamariscina</i>	37	52	15	0	0	2.52
Plot A. Backcross to monoecious parent						
F <sub>1</sub> ( <i>Amaranthus hybridus</i> Angol race × <i>Acnida tamariscina</i> ) × <i>A. hybridus</i> Angol race	255	14	3	7	9	
F <sub>1</sub> ( <i>Acnida tamariscina</i> × <i>Amaranthus hybridus</i> Angol race) × <i>A. hybridus</i> Angol race	1558	328	114	42	40	
Control. Normal <i>Acnida tamariscina</i> × <i>A. hybridus</i> Angol race	125	5	14	0	0	
Plot C. Backcross to monoecious parent						
F <sub>1</sub> ( <i>Acnida tamariscina</i> × <i>Amaranthus retroflexus</i> ) × <i>A. retroflexus</i>	54	0	0	6	0	
F <sub>1</sub> ( <i>Amaranthus retroflexus</i> × <i>Acnida tamariscina</i> ) × <i>A. retroflexus</i>	263	0	1	3	1	
F <sub>1</sub> ( <i>Amaranthus retroflexus</i> × <i>Acnida cuspidata</i> ) × <i>A. retroflexus</i>	6	0	0	0	0	

Use of the pollen from the male hybrids is not feasible, because the flowers usually do not open sufficiently to protrude the anthers, and the anthers usually fail to dehisce. As preliminary backcrossing attempts using the female hybrids yielded so few seeds per pollination, the use of isolation plots was necessary. Ten to 25 female hybrids were planted in each plot

together with the pollen producer which was either the dioecious or the monoecious parent. As noted previously, new flowers are continually produced in unpollinated inflorescences or where the seed set is poor. Consequently, a large hybrid plant at the end of the season may have had as many as a hundred thousand flowers and so would yield some seed despite the high sterility. Results from these backcross progenies are summarized in table 7.

Backcrosses to the dioecious parent (plots E and F) in the two cases studied give ratios of 1 ♀ : 1 ♂ with no more than the usual deviation. This result was expected because these are backcrosses to the epistatic sex condition. The neuter plants are due to the dominant factor carried in the dioecious parent, *Acnida tamariscina*. No significance can be attached to the proportion of neuter hybrids since several male plants were used as pollen producers. Part of these may have been free from this factor, part heterozygous for it, and part homozygous for it.

The results from backcrossing the F<sub>1</sub> female hybrids to the monoecious parent are shown in table 7, plot C. The results are essentially the same regardless of which way the F<sub>1</sub> cross was made, but the high proportion of females and low proportion of monoecious plants was not anticipated. If the segregation of chromosomes in the hybrid was completely random, gametes containing all possible combinations of the two chromosome complements should be secured. While many of these might be lethal, one should expect at least three kinds of functional gametes; namely, those having an entire genom originally obtained from the dioecious parent, those having an entire genom originally obtained from the monoecious parent, and those having both genoms. The first type of hybrid gamete after fertilization by a monoecious gamete should reconstitute the F<sub>1</sub> hybrid female, the second should reconstitute the monoecious parent and the third should produce a triploid plant with two monoecious genoms and one dioecious female genom. One can be reasonably certain that the third type of gamete is functional, otherwise doubling the chromosome complement of these hybrids ought not to restore fertility. The second type of gamete must be formed very infrequently because the monoecious plants, which occur, are sterile and phenotypically unlike the parental monoecious species. One cannot be sure about the first type of gamete since the phenotypic appearance of the resulting F<sub>1</sub> hybrids might be indistinguishable from the triploids. These second generation plants are remarkably uniform in all characters and while similar in appearance to the F<sub>1</sub> hybrids, their pubescence, leaf shape and habit approach more closely the characters of the normal monoecious parent, *Amaranthus retroflexus*. Somatic chromosome counts were made for 16 plants selected at random from the cross F<sub>1</sub> (*Acnida tamariscina* × *Amaranthus retroflexus*) × *Amaranthus retroflexus*.

All plants had the triploid number of 50 chromosomes which would be attained by the combination of one dioecious *Acnida* genom of 16 chromosomes with two monoecious *Amaranthus* genoms of 17 chromosomes each. Likewise, nine plants from the cross  $F_1$  (*Acnida tamariscina*  $\times$  *Amaranthus hybridus*)  $\times$  *Acnida tamariscina* have the expected triploid number of chromosomes,  $(16+16+16)=48$ . This is proof that the  $F_1$  hybrids produce only one principal type of viable gamete and that this gamete contains both genoms.

Progenies derived from plot A crosses differ from plot C crosses in having a considerable number of male and neuter plants. There must have been some dioecious pollen present in this plot since the control had five males. Chromosome counts of several females selected at random show that these plants have the expected triploid number of 48 chromosomes obtained from backcrossing to the monoecious parent. However, one neuter and one male definitely had 48 chromosomes which could be attained from backcrossing to the dioecious parent. Thus, the male and neuter plants found in these families probably should be disregarded. An equal number of the females should have been due to pollination with dioecious pollen. The corrected figures for plot A are 241 ♀ ♀ : 16 monoecious or a ratio of 15:1 and 1230 ♀ ♀ : 82 monoecious or a ratio of 15:1. In these two crosses the  $F_1$  hybrid female plants came from reciprocal crosses. Plot C has 323 ♀ ♀ : 10 monoecious or a ratio of 31:1.

It is difficult to evaluate the significance of these ratios and the presence of the monoecious plants. They have a near triploid constitution but this may not be a balanced complement. In so far as the vegetative parts of the plant are concerned, monoecious plants are indistinguishable from triploid females. The production of stamens is limited to the first flower of each flower cluster exactly as in the monoecious first type species. Ovary development may or may not be inhibited in these staminate flowers and this varies on the same plant. Some plants have all the first flowers of each flower cluster staminate or perfect (called normal monoecious); others have only a few of the first flowers staminate or perfect (called sporadic monoecious). With so much variability of expression, this enumeration may have little significance.

*Backcross of  $F_1$  colchicine-induced tetraploid hybrids obtained  
from "3" to both parental types*

A 0.25 percent aqueous solution of colchicine applied to the growing points induced tetraploid chimeras on several female hybrids and these areas with restored fertility were backcrossed to the parental species. The results are summarized in table 8.

TABLE 8

*Backcross of F<sub>1</sub> hybrid colchicine-induced tetraploid females (derived from intergeneric crosses) to parental types.*

CROSS	♀ ♀	♂ ♂	D./P.E.	
			1:1	1:2
Backcross to dioecious parent:				
F <sub>1</sub> ( <i>Acnida tamariscina</i> × <i>Amaranthus caudatus</i> Mexican race) × <i>A. tamariscina</i>	265	311	2.8	
F <sub>1</sub> ( <i>Acnida tamariscina</i> × <i>Amaranthus hybridus</i> Angol race) × <i>A. tamariscina</i>	26	28	0.4	
F <sub>1</sub> ( <i>Amaranthus hybridus</i> Angol race × <i>Acnida tamariscina</i> ) × <i>A. tamariscina</i>	50	49	0.3	
F <sub>1</sub> ( <i>Acnida tamariscina</i> × <i>Amaranthus caudatus</i> Manchurian race × <i>A. tamariscina</i> )	40	86	6.0	0.6
F <sub>1</sub> ( <i>Amaranthus caudatus</i> Manchurian race × <i>Acnida tamariscina</i> ) × <i>A. tamariscina</i>	108	114	0.6	
Backcross to monoecious parent:				
F <sub>1</sub> ( <i>Acnida tamariscina</i> × <i>Amaranthus caudatus</i> Mexican race) × <i>A. caudatus</i> Mexican race	238	0		
F <sub>1</sub> ( <i>Acnida tamariscina</i> × <i>Amaranthus caudatus</i> Manchurian race) × <i>A. caudatus</i> Manchurian race	69	0		
F <sub>1</sub> ( <i>Amaranthus caudatus</i> Manchurian race × <i>Acnida tamariscina</i> ) × <i>A. caudatus</i> Manchurian race	6	0		

Backcrosses to the dioecious parent gave ratios of 1 ♀ : 1 ♂ and these plants have the expected triploid number of 48 chromosomes. Progenies derived from backcrosses to the monoecious parent consist exclusively of female plants and nineteen plants selected at random have the expected triploid number of 48 chromosomes. These backcross progenies are similar to the untreated backcrosses except that monoecious plants are not found.

#### DISCUSSION

It has been shown that a cross of an *Acnida* female of a dioecious species to a monoecious "first type" species gives only females and that the reciprocal cross gives an equality of males and females. Since the male is the heterogametic sex, the sex mechanism of these three dioecious species is, therefore, of the XY type. These crosses also give a direct comparison of the female genom X + 15A to the male genom of Y + 15A as the monoecious genom is identical in both cases. If the assumption is made that the autosomes exhibit random distribution in the formation of gametes and are either homozygous for all sex factors or lack of such factors, one may conclude that the sex chromosome pair (XY) contains the differential genic mechanism which initiates the development of maleness or femaleness in an individual sporophyte under normal conditions. If the auto-

somes contain sex factors and are not homozygous for them, segregation should occur in the inbred lines of the dioecious species as well as in the crosses to the related dioecious and monoecious species. However, there is no evidence of segregation either within the species or in the interspecific hybrids. If random distribution of the autosomes does not occur, abnormal ratios for two autosomal genes should be secured, but are not. This interpretation cannot be considered absolute proof that the Y chromosome carries the male-determining factors. However, if the *Drosophila* type of sex inheritance were true of Acnida, one should expect the XXXY (3X+4A) tetraploid Acnida males to be intersexes.

Since intersexes, hermaphroditic plants or sexual abnormalities are not found in the second generation progeny of an interspecific cross of two different dioecious species, the genic sex mechanism is apparently identical in both species. The interpretation is made that such exact similarity would be unlikely if sex were due to the interaction of a large number of genes.

TABLE 9  
*Genotypic balance in relation to sex.*

DIPLOID	TRIPLOID	TETRAPLOID
Pure Species:		
$d d = \text{♀}$		$d d d d = \text{♀}$
$D d = \text{♂}$		$D d d d = \text{♂}$
		$D D d d = \text{♂}$
$m_1 m_1 = \text{mon.}_1$		$m_1 m_1 m_1 m_1 = \text{mon.}_1$
$m_2 m_2 = \text{mon.}_2$		
Hybrids:		
$d m_1 = \text{♀}$	$d m_1 m_1 = \text{♀}$	$d d m_1 m_1 = \text{♀}$
$D m_1 = \text{♂}$	$d d m_1 = \text{♀}$	$D D m_1 m_1 = \text{♂}$
$d m_2 = \text{♂}$	$D d m_1 = \text{♂}$	
$D m_2 = \text{♂}$	$d m_1 m_2 = \text{♂ or mon.}^*$	$d d m_2 m_2 = \text{mon.}_2^{**}$
$m_1 m_2 = \text{mon.}_1^*$		
Where $d = \text{♀}$ genom of dioecious species	$m_1 = \text{genom of monoecious species first type}$	
$D = \text{♂}$ genom of dioecious species	$m_2 = \text{genom of monoecious species second type}$	

\* Sometimes intermediate.

\*\* Only one plant observed.

The dioecious and monoecious "first type" species used in this work do not enable one to study directly the genetic basis of the evolution of sex. However, it is possible to compare several combinations of genoms and their relation to sex (table 9).

It is shown, in the present work, that males are formed if one male genom of *Acnida* is present with one monoecious first type genom of *Amaranthus*, and that females are formed when one female genom of *Acnida* is present with one or two monoecious genoms of *Amaranthus* and only in the absence of a male genom. MURRAY (unpublished) has shown, from a study of tetraploids of *Acnida tamariscina*, that malesness is induced when one male genom is present with one or even three female genoms.

The combination of a single female genom of *Acnida* with a genom of the monoecious second type species of *Amaranthus* usually results in malesness although occasionally the males produce a few pistillate flowers near the base of the plant. In addition a few females have been observed. It has been assumed that factors inducing malesness in the second type monoecious plant are generally epistatic to the factors inducing femalesness. When a female genom, a monoecious first type genom, and a monoecious second type genom are combined in a triploid, the result is either a male plant or a monoecious one without any precise positional arrangement of the pistillate and staminate flowers. This peculiar type of monoecism has been observed in these triploid progeny only when the monoecious first type genom is that of *Amaranthus hybridus* Angol race. The same result is obtained in a diploid hybrid when a genom of the Angol race is combined with one of the second type of monoecism. Other species of the first type of monoecious arrangement are completely epistatic over the second type; and the addition of a single female genom of *Acnida tamariscina* to these diploids results in the formation of triploid males. Whether these phenotypic effects are due to many or only a few genes cannot be stated.

The intergeneric  $F_1$  hybrids between dioecious and monoecious first type species produce only one type of functional gamete and this contains the diploid number of chromosomes including both parental genoms. These gametes probably arise from the reconstitution of the chromosomes into one nucleus after an abortive first division. MANGELSDORF and REEVES (1939) have observed the same phenomenon in the intergeneric hybrids of *Zea*  $\times$  *Tripsacum* where the only functional gametes are those possessing both genoms.

It has been shown that the presence of barely viable hybrids in the crosses of *Acnida tamariscina* to *Amaranthus spinosus* are found only in certain crosses and not in others and that their presence is probably conditioned by a single factor carried in the dioecious species. This phenomenon may be of general occurrence in wide crosses. MANGELSDORF and REEVES (1939, pp. 89, 103) have reported vigorous and dwarf  $F_1$  hybrids in the intergeneric crosses of *Zea*  $\times$  *Tripsacum*. They also cite examples in *Fragaria* hybrids and in sorghum-sugarcane hybrids. Since these species

are probably highly heterozygous, the same type of explanation may very well apply.

The presence of neuter hybrids in certain crosses between *Acnida tamariscina* and all monoecious first type *Amaranthus* species constitutes a new kind of isolation mechanism. These species will hybridize readily if growing in the same area, but hybridization could not be carried beyond the first generation since in certain lines all the  $F_1$  hybrids are neuter plants. This mechanism is supplemented by the low degree of fertility of the hybrids which flower. It has been shown that either *Acnida tamariscina* males or females may carry the dominant neuter-inducing factor in either a homozygous or heterozygous condition, and appear phenotypically normal. Neuter hybrids are obtained only on outcrossing to one of the monoecious first type species. The factor is shown to be linked to a color gene with 1.4 percent crossing over, and when heterozygous induces 50 percent pollen abortion and presumably 50 percent ovule sterility. This suggests that the factor is probably related to, or due to, a translocation or an inversion rather than a point mutation. Phenotypically neuterness results in the suppression of flowers of either sex, although not always in the same proportion. Any direct relation to the mechanism of sex determination or evolution of sex is not apparent.

#### ACKNOWLEDGMENTS

The author is indebted to PROFESSOR R. A. EMERSON and PROFESSOR L. W. SHARP for their guidance throughout the problem, to PROFESSOR L. F. RANDOLPH for criticism of the manuscript; and to Dr. P. C. STANDLEY of the Field Museum of Natural History for identification of the material.

#### SUMMARY

In this study of the genetics of sex determination, three dioecious species of the genus *Acnida* and five monoecious species (eight races) of the genus *Amaranthus*, family *Amaranthaceae*, have been used. The monoecious species exhibit two types of distribution of the male and female flowers, although the growth pattern of the inflorescence of all species, regardless of sex, is identical.

Included in this paper are the results of an investigation of 29 interspecific and 33 intergeneric  $F_1$  hybrids; the production of tetraploid races in one dioecious and two monoecious species; the creation of five amphidiploid races; and an analysis of about 6000 second generation progeny obtained from backcrossing  $F_1$  intergeneric hybrids to the parental species. Altogether, over 50,000 plants were used.

Genetical data indicate that the male *Acnida* plant is heterogametic. The hypothesis is advanced that the XY chromosome pair in the dioecious

species carries the differential sex factors and that the autosomes, if they carry sex factors, are homozygous for them not only within the species, but also in different species.

Several diploid, triploid, and tetraploid combinations of dioecious and monoecious genoms have been studied. These data show that the complex of sex factors in the Y chromosome are epistatic to those in the X chromosome and to those in a monoecious genom. Likewise, the factor, or factors, in the X chromosome are epistatic to those in the monoecious "first type" genom but are hypostatic to those in the monoecious "second type" genom.

Neuter plants, wherein the flower primordia fail to develop, occur among certain F<sub>1</sub> intergeneric hybrids. This condition is shown to be due to a single dominant autosomal factor present in the species *Acnida tamariscina* and *only expressed* when outcrossed to any of the monoecious "first type" species. The neuter factor is linked to a color factor (1.4 percent C.O.) and when heterozygous is associated with 50 percent pollen abortion. This suggests that the factor may be carried on a translocated or inverted region. The development of flowers of both sexes is inhibited by the neuter phenotype, so that there is probably no direct relationship to the mechanism of sex determination.

The hybridization of certain *Acnida tamariscina* plants with *Amaranthus spinosus* results in the production of barely viable hybrids. Progenies may contain all non-viable, 50 percent non-viable, or all viable hybrids. A single dominant factor, perhaps identical to the neuter-inducing factor, apparently conditions the production of barely viable hybrids. The neuter-inducing factor and also the non-viability factor (if different) are tentatively cited as new physiological types of isolation mechanisms.

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