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A GENETIC STUDY OF VARIATIONS IN FLORAL MORPHOLOGY AND FUNCTION IN CULTIVATED FORMS OF VITIS

GEO. D. OBERLE

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ABSTRACT

GRAPE flowers are of three rather sharply defined types; viz., functionally hermaphroditic, functionally pistillate and functionally staminate. All types are morphologically hermaphroditic, however, in that flowers of each class have full complements of stamens and pistil. Unisexualism has resulted from abortion of either the male or female sexual elements in the normal bisexual type. Abortion of the sexual elements occurs during a late stage of their development and always after meiosis. American species of Vitis are entirely dioecious in that only staminate and pistillate individuals occur. The same has been found to be true of all other species of Vitis with the exception of European and Asiatic V. vinifera, which has functionally hermaphroditic as well as functionally pistillate and staminate forms.

The three flower types are genetically determined. Abortion of the male sexual elements, resulting in the unisexual pistillate type, is the result of a recessive factor *sp*. Abortion of the female sexual element, resulting in the unisexual staminate type, is governed by a dominant factor *So*. Though these are separate and distinct factors both are carried on the same chromosome and occupy positions which do not permit crossing over between them. The following genetical formulae are assigned to the various floral types:

$\frac{\text{so sp}}{\text{so sp}}$ = functional pistillate

$\frac{\text{So Sp}}{\text{so sp}}$ = functional staminate

$\frac{\text{so Sp}}{\text{so sp}}$ = heterozygous hermaphrodite

$\frac{\text{so Sp}}{\text{so Sp}}$ = homozygous hermaphrodite

$\frac{\text{So Sp}}{\text{so Sp}}$ = "derived" functional staminate

Crosses involving the various floral types exhibit simple Mendelian ratios. A few hermaphroditic individuals are homozygous for hermaphroditism in that when selfed or crossed with other hermaphroditic or pistillate individuals only hermaphroditic progeny result. Other hermaphroditic forms are heterozygous for hermaphroditism in that when selfed or intercrossed they give 3 : 1 ratios of hermaphroditic to pistillate offspring. When backcrossed to the double recessive pistillate form 1 : 1 ratios of hermaphroditic to pistillate progeny result. Staminate forms appear only in progeny from crosses involving a staminate parent.

Mendelian ratios calculated for the various combinations of crosses show close agreement with observed ratios.

Functional hermaphrotitism is considered to have been the primitive floral type in Vitis. Unisexualism is phylogenetically younger and has been derived from the bisexual condition. A theory is presented which accounts for the evolution of dioecism from functional hermaphroditism.

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A GENETIC STUDY OF VARIATIONS IN FLORAL MORPHOLOGY AND FUNCTION IN CULTIVATED FORMS OF VITIS[1]

GEO. D. OBERLE[2]

INTRODUCTION

IN view of the interest being shown at present in the breeding of improved forms of fruits, a more detailed knowledge of genetic facts pertaining to the mode of inheritance of specific characters of the types entering into the crosses should be of theoretical interest to the geneticist and of significant practical value to the fruit breeder. The grape has received at least as much attention from fruit breeders as any other fruit, but to date only a few characters have received genetical analysis and in most of these instances the interpretations have not been entirely satisfactory. An extensive grape breeding program has been conducted at this Station for nearly 50 years. Private investigators have carried on breeding work with this fruit for nearly a century. Tho the results of these programs have been successful from the standpoint of production of new varieties and improved types, there is at present a pronounced dearth of available information on genetical studies dealing with this plant. In order that this apparent lack of genetical information might be partially overcome, a problem dealing with the heredity of some important and useful character was sought for study.

Of the characters of the grape considered for this study, that of floral morphology as it is concerned with the development and function of the sex organs seemed most suitable. As will be shown later in this discussion, this character is closely associated with the manner in which the flower is able to function in reproduction. This character

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[1] The material in this bulletin was presented to the Faculty of the Graduate School of Cornell University in June 1938 in partial fulfillment of the requirements for the degree of doctor of philosophy.

[2] The author takes this means of expressing his sincere appreciation to Professor Richard Wellington who suggested the problem, advised during its solution, and who placed at the disposal of the author the facilities of the breeding vineyards of the New York State Agricultural Experiment Station at Geneva as well as the vineyard notes compiled in the past by members of the Pomology Division and also to Professor R. A. Emerson of Cornell University whose aid in the genetical analysis of the data and whose criticism of the manuscript have been most helpful.

is of importance to the practical grape grower because of its influence on yields. It is of interest to the grape breeder because it influences the manner in which certain crosses can be made. It shows rather sharply delimited segregation, is constant in its perpetuation, and its various forms of expression are easily classified. Furthermore, this character is of interest because of its relation to the origin of the cultivated grapes of today and to the species problem of the wild and cultivated forms.

The matter of floral morphology in the grape has long been the object of study by both viticulturists and botanists. Viticulturists have confined their observations mainly to normal floral morphology, but botanists have paid special attention in recent years to variations in the floral morphology.

A thoro and satisfactory descripition and classification of variations in floral morphology of the grape has been given by Dorsey (1912).[3] He regards the genus Vitis as being dioecious, polygamodioecious, or perfect. Individual vines of species native to America were found to occur in either the staminate or the pistillate form only. Among wild-growing vines the staminate individuals were found to occur in the greater number. The perfect-flowered form has the normal complement of five erect stamens surrounding a stout bottle-shaped pistil. The pistillate flowered form has the normal number of stamens surrounding the pistil, but the former members are recurved to a position below the base of the ovary. The staminate flower possesses the normal complement of erect stamens, but the pistil is so much reduced as to appear to be entirely lacking, and only rarely is the stigma present and discernible. Close observation, however, reveals the rudiments of the pistil which may or may not have a stigmatic surface. The recurved stamens of pistillate flowers have sporogenous tissue and produce abundant pollen which, however, is nonviable. The rudimentary pistils of the staminate flowers when sectioned reveal the normal complement of two carpels each having two abortive ovules.

REVIEW OF LITERATURE

According to Hedrick (1908), Walter was the first to report on the occurrence of masculine and feminine forms of grape flowers in describing American species of grapes in 1778. Bartram in 1804 also spoke of hermaphroditic or female and barren or male flowers in describing American grapes. De Candolle (1830) recognized two classes of grapes, the hermaphroditic species native to the Old World, and the dioecious or polygamous species native to America. Rafinesque (1830) also remarked of the occurrence of three floral types of grape flowers.

Bronner (1857) observed staminate and fruitful and unfruitful hermaphroditic grape flowers on wild plants in the Rhine Valley. The recurved stamens of the unfruitful hermaphrodites were described as appearing sterile and the opinion was advanced that the function of the male plants was to fertilize the unfruitful hermaphrodites. Wylie (1871) recognized the necessity of using pollen from staminate flowers of *Vitis rotundifolia* on the pistils of other species in attempting to breed improved Muscadine grapes. The imperfect hermaphrodites he found were unable to act in cross pollination except as the female parent.

Munson (1886) reported upon the inability of reflexed stamen types of grape flowers to set fruit when self pollinated, but stated that they did set good crops of fruit when cross pollinated with pollen from hermaphroditic or staminate vines. He drew attention also to the fact that all species native to America are strictly dioecious and raised the question of the origin of certain hermaphroditic varieties (Concord, Herbemont, Catawba, etc.) which were supposedly pure American species. In later publications (1900, 1909), he recognized only three types of grape flowers and advanced the theory that dioecism developed rather recently from the hermaphroditic condition.

The credit for obtaining the first scientific proof of variation in the function of the recognized types of Vitis should probably be awarded to Rathay (1888–1889). This investigator found that normally any one grape plant carried only one of the three recognized floral types. Microscopic study of the pollen grains showed those from the anthers of pistillate flowers to be spindle shaped and devoid of germ pores and the triradiate ridge of the tetrad scar, whereas pollen grains from anthers of staminate or hermaphroditic flowers were keg shaped and had both germ pores and tetrad scars. The former type of pollen grains were never observed to produce pollen tubes, whereas pollen grains of the latter type produced long, vigorous pollen tubes when germinated in sugar solution.

Rathay recognized that dioecism in grapes resulted from one or the other of the sex organs of a basic hermaphroditic type becoming rudimentary and nonfunctional. A survey of 78 varieties grown in the vineyards at Klosterneuberg showed 42 were perfect flowered and 36 were pistillate flowered. The latter group invariably proved to be lower yielding than the varieties constituting the perfect-flowered group. The importance of selecting the latter types for the vineyard was emphasized as was the necessity of interplanting the pistillate types, when the latter must be grown, with suitable perfect-flowered types having the same bloom period in order to insure satisfactory cross pollination. Bagging tests were made to confirm these statements.

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[3] Figures in parenthesis refer to "Literature Cited," page 58.

Rathay made the first report on the breeding behavior of the various flower types. He obtained both hermaphroditic and pistillate flowered offspring from the seed of selfed hermaphrodites but with a few rare exceptions no males. He conjectured that seed from pistillate flowers pollinated with hermaphroditic pollen should give only hermaphrodites but had no proof for the belief. The importance of using pollen from hermaphrodites in breeding programs in order that a higher proportion of the progeny might be hermaphroditic was mentioned. He recommended that pistillate flowered types be used as the female parent since such flowers would not require emasculation. No hermaphrodites were found among wild populations. He concluded that the perfect flowered forms arose from staminate forms thru the influences of cultivation which stimulated the pistils to develop. However, he observed that perfect-flowered forms in abandoned vineyards do not lose this character when neglected in cultural care and concluded that the hermaphroditic character must have become well fixed. He concluded ". . . . the dioecious wild grapes transform themselves . . . . under the influence of cultivation into gynodioecious plants in that in the flowers of the staminate individuals the pistils become fully developed whereas in the flowers of the pistillate individuals the stamens remain in their rudimentary condition. . . . It seems likely that the unisexual flower was derived from the bisexual flower which was the primitive type . . . . and that the male individuals under cultivation became hermaphroditic. That this latter did not occur also with the female flowers is a most important and unexplained fact."

Oberlin (1889), too, reported that the wild *Vitis sylvestris* of central Europe is always dioecious. Millardet (1889) obtained no germination in sugar solution of pollen from pistillate-flowered types of numerous species of Vitis. Green (1893) showed by bagging experiments that varieties having reflexed stamens were unable to set fruit with their own pollen, whereas varieties having upright stamens set fruit abundantly when bagged. Engelmann (1895) emphasized that dioecism prevailed in all American species of Vitis, but that both flower types were morphologically hermaphroditic by virtue of having the organs of both sexes, tho one or the other was always nonfunctional.

Beach (1898, 1899 1902) by means of bagging tests showed that recurved stamens were associated with self-sterility. Pollen from such varieties was usually incapable also of cross fertilizing other varieties, tho he reported obtaining occasional seeded fruits from the use of such pollen.

Booth (1902) found the impotent pollen to differ in shape from that of upright stamens and that it tended to remain clumped in tetrads. He expressed the opinion that the staminate and pistillate forms were in the process of evolution from the hermaphrodite to the dioecious state.

Basserman-Jordan (1907) considered the wild dioecious grapes of the Rhine Valley to be distinctly different from the Asiatic *V. vinifera* and preferred to give the former specific rank as *V. sylvestris*. Andrasovsky (1925) considered the cultivated grapes of Europe not to represent a unit species or subspecies but rather a heterogeneous group derived from five well-defined species and their hybrids. The species in central Europe he called *V. allemanica;* the race in southern Europe *V. mediterranea;* and those in western Asia *V. antiquorum*, *V. byzantina*, and *V. delicosa*.

Viala and Péchoutre (1910) commented on the fact that no male vines appeared in crosses among cultivated varieties of *V. vinifera*.

Reimer and Detjen (1910) reported finding a wild dark-fruited muscadine vine (*V. rotundifolia*) with hermaphroditic flowers, the pollen of which proved to be 95 per cent germinable. However, the pistils were smaller than those of pistillate vines, and set only light crops of fruit.

Dorsey, in addition to the study on floral morphology (1912) already mentioned, reported (1914) on cytological studies of pollen development with special reference to sterility. The various stages in meiosis were found to occur regularly and similarly in the pollen mother cells of both pistillate and hermaphroditic forms up to the first division of the microspore nucleus. Then in the microspores of pistillate flowers the nucleus either failed to divide to give the normal vegetative and generative nuclei or, if division did take place, the generative nucleus at once degenerated. In normal pollen from flowers with upright stamens the division of the microspore nucleus occurred normally to give normal vegetative and generative nuclei. Study of the ovules of the rudimentary pistils of staminate flowers showed the ovules to be normal except that the tissue which in normal ovules developed into the seedcoats was very scanty and degenerated early in its development. The filaments of the reflexed stamens were studied anatomically and were found to have the normal vascular elements. However, the cortical cells on the dorsal (outer) surface of the filament were found to have conspicuously thinner walls than comparable cells on the opposite side of the filament. This feature was considered to be responsible for the reflexing tendency of such stamens.

Husman and Dearing (1913) reported finding two hermaphroditic-flowered seedlings of Muscadine grapes. Both were self-fertile and set good crops. Dearing (1917) reported selfing one of these seedlings and getting about 85 per cent hermaphroditic progeny. Crossing the hermaphrodite on pistillate types gave progeny which were in the ratio of one pistillate to one hermaphrodite. No males occurred in the progeny from crosses of these types. Detjen (1917, 1919a, 1919b) reported similar results from the use of a hermaphroditic Muscadine seedling in his breeding for more fruitful Muscadine grapes.

Anthony (1914) and Hedrick and Anthony (1915) were the first to report on the inheritance of flower types and sex in grapes and to attempt to formulate a Mendelian explanation for their results. They found that most hermaphrodites when selfed or intercrossed gave about 20 per cent pistillate and 80 per cent hermaphroditic progeny. Pistillate-flowered types when crossed with pollen from hermaphrodites gave about one-half pistillate to about one-half hermaphroditic offspring. A few seedlings were obtained from selfing pistillate-flowered forms and by the use of their pollen on pistils of hermaphroditic forms. Male vines appeared, with rare exceptions, only when a staminate parent entered into the cross. However, the theory of inheritance presented was entirely inadequate in the light of modern genetics and cytology. Their explanation has been criticized by Rasmussen (1916), Valleau (1917) and Malloch (1923). The latter two men, using the data of Hedrick and Anthony, formulated theories of inheritance of their own which were no less inadequate than that of Hedrick and Anthony.

Stout (1921) reported observing all degrees of relative development of stamens and pistils in grape flowers. These variations in the relative development of the sex organs he described as phenomena of intersexualism. Weak grades of femaleness were considered to be responsible for the development of seedless fruits, while still another grade of femaleness was considered to be responsible for near seedlessness. A previously unreported type of pollen-sterile grape flower with erect but "crinkled" stamens was described. Pollen from recurved stamens was found to be incapable of germination on agar media. Later studies (1936, 1937) showed that in certain grapes seedlessness results from abortion of the embryo sacs and ovules after apparently normal development in the early stages. In others seedlessness results from abortion of the embryo after fertilization. The conclusion was drawn that the causes of the abortion reside in the haploid generation and arise after the reduction division. The abortions were considered to be of a hereditary nature and the result of factor segregation. Olmo (1935) found empty seededness to be the result of embryo abortion at an early stage of development. The character was found to be of a hereditary nature and governed by recessive factors which produced evident effects only thru the female parent.

Tupikov (1927) also considered the differences between staminate and pistillate forms to be quantitative rather than qualitative in nature deriving his opinion from observed variations in morphological development of pistils and stamens.

Stuckey (1923) reported that pollen from pistillate Muscadine vines develops normally until the pollen grains are well formed, after which the generative nuclei abort.

Muller-Thurgau and Kobel (1924) presented a hypothetical scheme for the inheritance of sex in grapes. They assumed each flower to be morphologically hermaphroditic with dioecism resulting from two pairs of factors affecting the development of the sex organs.

K = inhibitor of pistil development
k = normal pistil
S = normal stamens
s = inhibitor of stamens
$kk\ \ ss$ = female
$Kk\ \ Ss$ = male

$$\overset{\text{♀}}{kk}\ ss\times \overset{\text{♂}}{Kk}\ Ss=\begin{cases}1\ kk\ ss=\text{♀}\\ 1\ Kk\ Ss=\text{♂}\\ 1\ kk\ \ Ss=\text{⚥}\\ 1\ Kk\ \ ss\ \text{neutral and probably lethal and never observed}\end{cases}$$

$$\overset{\text{⚥}}{kk}\ Ss\times \overset{\text{⚥}}{kk}\ Ss=\begin{cases}\left.\begin{array}{l}1\ kk\ SS=\text{⚥}\\ 2\ kk\ \ Ss=\text{⚥}\end{array}\right\}3\\ 1\ kk\ \ ss=\text{♀}-1\end{cases}$$

Other possible genotypes were presented as follows:

$Kk\ \ SS=\text{♂}$ $\quad$ $kk\ \ Ss=\text{⚥}$
$KK\ \ SS=\text{♂}$ $\quad$ $kk\ \ SS=\text{⚥}$
$KK\ \ Ss=\text{♂}$ $\quad$ $KK\ \ ss$ = neutral and probably lethal
$Kk\ \ ss$ = neutral and probably lethal

Certain possible crosses of hermaphrodites or pistillate forms by males should give only male offspring according to their scheme.

$$kk\ \overset{\text{⚥}}{Ss}\times KK\ \overset{\text{♂}}{SS}=1\ \overset{\text{♂}}{Kk}\ ss:1\ \overset{\text{♂}}{Kk}\ Ss$$

No explanation was offered for this type of cross and no data were presented to support their theory.

Williams (1923) found evidences of somatic segregation of anatomical stem characters in hybrids of *V. rotundifolia* by species of Euvitis and suggested that the appearance of both male and hermaphroditic flowers on the same plant might be due to somatic segregation of these characters.

Baranov (1927 b, c) reported finding otherwise normal vines of the variety Mourvèdre (*V. vinifera*) the flowers of which were at all stages of their development, without vestiges of stamens. He termed these flowers to be morphologically perfect females. Correns (1928), however, considered them to be nothing other than an example of paragynodioeciousness in that the abortive anthers, which were enclosed within an enveloping carpel, were being gradually transformed into ovules. Baranov (1927a) studied the wild grapes of Tashkent and found only pistillate- and hermaphroditic-flowered types. Since no males were found he considered them to be escapes from cultivation rather than indigenous forms. Popov (1929) corroborated this report and theory. Vavilov (1930) however, reported finding in Georgia, Armenia, and Azerbaijin various indigenous sorts of grapes (*V. vinifera*) which demonstrated the entire known scale of diversity in flower form, color and size of fruit and in size of seeds.

Hirayanagi (1929) reported the haploid chromosome number in several species of grapes to be 19. In no case was he able to detect differences in the sizes or shapes of the chromosomes of male, female, or hermaphroditic types which might be construed as a sex chromosome mechanism. These results were later confirmed by Kobel (1929a, 1929b), Nebel (1929), Sax (1930), Negrul (1930), Husfeld (1932), Branas (1932), Ghimpu (1932), Angelo and Becker (1934), Wanscher (1934), Olmo (1937), and others. Altho all reported 38 to be the prevailing somatic number in species of Euvitis, Sax found the somatic number of *V. rotundifolia* to be 40. He found also one seedling of a Chinese variety to have 40 chromosomes. Husfeld, too, reported finding two seedlings with the latter number. Nebel reported gigas forms of Sultanina and Muscat to be tetraploids with 76 chromosomes. Olmo (1936, 1937) likewise reported gigas tetraploid forms of Sultanina, Cornichon, Muscat of Alexandria, and Tokay and in addition several triploid seedlings with 51 chromosomes.

Kobel (1929a, 1929b, 1933) made cytological study of the degenerating pollen grains of pistillate-flowered grapes and of the degenerating eggs of staminate flowers. In both cases the development was normal thruout the reduction division, the degeneration occurring in the early divisions of the microspore and megaspore nuclei. Lazarevsky (1932) made similar studies of the development of the embryo sacs of the variety Chasselas Gros Coulard which, tho it blooms heavily, always gives poor sets of fruit regardless of the source of pollen or environmental conditions. The earlier stages in the development of the embryo sacs preceding the binuclear stage proceeded normally, but abortion took place between the binuclear and octonuclear stages. Only a small proportion of the embryo sacs showed normal development to which was attributed the unfruitfulness of the variety.

Wellington (1930a, 1930b, 1932, 1937) and Snyder (1932, 1935) reported on the segregation of floral types in the progeny of crosses involving *V. vinifera*. Wellington reported that Muscat Hamburg gave only hermaphroditic seedlings regardless of the flower type of the other parent entering into the cross and considered this variety to be homozygous for the character of upright stamens.

Lawrence (1931) and Wanscher (1934) reported finding examples of secondary association of chromosomes in studying metaphase plates of grape microsporocytes and concluded that the somatic number of 38 was not a primary one. Both workers considered the grape to be polyploid and predicted complex heredity of characters.

The ability of pollen from reflexed stamens to germinate and to fertilize pistillate or hermaphroditic flowers has been investigated by Korchinsky (1910), Gard (1913), Rasmuson (1916), Stout (1921), Prinz (1925), Seeliger (1925), Susa (1926), Steingruber (1927), Ziegler and Brandscheidt (1927), Iwanowa-Parauskaja (1929), Einset (1930), Dalmasso (1934), Wanner (1934), Kaczmarek (1938), and many others. All agreed that such pollen germinated very rarely if ever at all, and Stout, Iwanowa-Parauskaja, Susa, Gard, and Kaczmarek went so far as to state that pistillate pollen was never capable of germination.

Negrul (1936a, 1936b, 1936c) presented a monofactorial scheme of sex inheritance employing a quantitative difference in male and female sex potencies. Nebel (1936) also presented a monofactorial scheme of sex inheritance dependent on the activity of quantitative inhibitors of maleness and femaleness. Breider and Scheu (1938) presented a scheme of heredity of sex in grapes based on an XX—XY type of sex chromosome mechanism. They, too, assumed differences in the sex potencies of the sex chromosomes from various species and the ability of genotypically male and female forms to behave as hermaphrodites.

Wellington (1932) expressed the belief that all hermaphroditic American varieties of bunch grapes must have obtained their upright stamens by virtue of being not pure native species but rather hybrids of those species and *V. vinifera*. The breeding behavior of Concord, Lutie, Clinton, and Champion, varieties once considered to represent pure species, indicated segregation of characters of *V. vinifera*. Goethe (1887) had expressed similar beliefs. Bailey (1934) also raised the question of the ancestry of the hermaphroditic flowered varieties of American bunch grapes.

MATERIALS

The observations reported in this study were made upon the grape vines growing in the breeding vineyards of this Station at Geneva. Several thousand seedlings of known parentage were growing in the vineyard during the season of 1937. Of these many were flowering for the first time. In addition to the seedling plants studied, observations were made in the specimen vineyard which contained representative plants of the majority of the cultivated American varieties of bunch grapes and of many of the important varieties of European wine grapes (*V. vinifera*). Representatives of the following native species were also included: *Labrusca*, *aestivalis*, *vulpina*, *rupestris*, *Baileyana*, *Arizonica*, *cinerea*, *cordifolia*, *Simpsonii*, *Treleasii*, *Longii*, *solonis* and *Doaniana*. *V. amurensis* and *V. Coegnetiae* introduced from China and Japan respectively were also represented.

In addition to the vineyard material the author had access to the breeding records, including the plant descriptions, of all seedlings produced in the earlier breeding work of the Station.

In the data presented in this paper 68 named American varieties of cultivated grapes, 18 varieties of *Vitis vinifera*, 108 Station seedlings, and 6 pure American species have been employed as parents. A total of 716 parental combinations, including 103 selfed populations, are represented in the data presented. In addition, many more crosses have been made, but the populations produced were so small or the parental varieties of so little importance that their inclusion would not have justified the additional time and space necessary to include them.

TERMINOLOGY

As may be observed in the literature review, there is a common practice in speaking of grape vines to refer to them as being male or female. The former term refers of course, to those which are functionally staminate; while the latter term is applied indiscriminately to those which are capable of bearing fruit regardless of whether they were functionally pistillate or hermaphrodite. These fruitful females were generally recognized as being either self-fruitful or self-sterile. More recently the terms staminate, pistillate, and hermaphrodite have been generally applied in referring to these types, probably because of the objections to the application of sexual terms to the asexual generation.

In the opinion of the author, neither of the examples of nomenclature given is entirely correct nor wholly desirable. From the evidence at hand one may conclude that all grape flowers are hermaphroditic. This statement is fully as true of the staminate and pistillate forms as of the true hermaphroditic flowers. Each flower, whether it be staminate or pistillate in its function, possesses, in addition to its normally developed organs of one sex or the other, the rudimentary or incompletely developed organs of the opposite sex. In case of the pistillate vine the stamens, tho reflexed, are easily recognized as such and are readily apparent. The fact that the anthers borne on such stamens produce pollen in considerable amounts which develops normally, so far as can be ascertained, up to the stage in which the generative nucleus prepares for division into the two male gametes, indicates that these organs are not merely remnants of organs which have lost all semblance of sexual activity, but rather, organs of near normal development of which the functions are being suppressed at a rather late stage of their activity.

Similarly, in the staminate-flowered individuals, each flower possesses, in addition to the erect functional stamens, a full complement of incompletely developed ovules. Cytological observations by several workers, who have already been cited, have demonstrated that in such flowers the ovules produce normal macrospores which develop normally until after the stage in which the nucleus makes its first division to form the embryo sac, after which the embryo sac nuclei abort. Here again the elements of the sex opposed to the functional one are present and possess the capability of behaving normally up to a very late stage of their development. To be sure the phenotypic expression of the incompletely developed pistil is much less apparent than in the case of the incompletely developed stamens of the pistillate-flowered forms. In fact, in the majority of the so-called staminate forms the pistil appears to be entirely lacking, being represented by only a rounded pad or cushion of tissue which may or may not be surmounted by a rudimentary stigma. The style is entirely lacking in most cases. The true nature of the inconspicuous pad of tissue is revealed only by means of sectioning and cytological study.

The true functional hermaphroditic form of course possesses both a normally developed pistil and erect stamens with normal anthers.

There is considerable variation in the amount of recurving shown by the stamens of flowers borne on different pistillate-flowered individuals. In some individuals the stamens show a strongly marked recurving and twisting of the stamens, while in others the degree of recurving is much less marked. Likewise, the duration of time necessary for the recurving to become complete varies considerably. In some of the cases observed the folded stamens did not straighten out their filaments after shedding the corolla but at once snapped back to a reflexed and tightly twisted position inferior to the floral disk. In other cases the reflexed stamens curved back much more slowly, the filaments meanwhile completely extending themselves so that at one stage of their recurving the stamens radiated out from the base of the pistil similar to spokes of a wheel from the hub. Environmental conditions at the time of anthesis appeared to influence the rapidity of recurving and also its degree. On bright warm days the shedding of the corolla and recurving of the stamens required only a few minutes on some plants. On cloudy and damp days on the other hand, the corolla was not only shed much more slowly but the recurving of the anthers was much less rapid and less pronounced. Apparently the act of anthesis and reflexing of the stamens is conditioned by a dehydration process.

Several authors have reported similar variations in the degree of development of the pistils of staminate flowers. Dorsey (1912) speaks of several wild vines in which the flowers showed fairly well developed pistils and stigmas tho they set no fruit. Another instance is recited of a staminate hybrid (*riparia*×*labrusca*) vine which, in 2 years out of 30, bore light crops of fruit. The same author speaks also of a seedling Marion×Pocklington vine, the flowers of which functionally were so nearly intermediate between staminate and pistillate forms that on the same cluster some pistils had sufficient stigmatic surface to permit pollen germination while other flowers did not. Stout (1921) also reported the finding of considerable variation in the degree of pistil development in staminate flowers. He observed also functionally pistillate flowered forms with erect stamens which produced only sterile pollen in the one season tested. He looked upon such variations as examples of intergradation from staminate to pistillate forms and applied the term intersexes to such individuals. Negrul, Nebel, and others also spoke of intersexual types of grape flowers.

During the course of the observations reported in this paper, the author observed several cases of floral variation similar to those described above. Two seedling vines [(Keuka×Sultanina) and (Muscat Hamburg×Hubbard)] bore flowers having erect stamens and extremely weakly developed pistils. In some clusters every flower appeared to be devoid of stigma or pistil while in other clusters fairly well developed pistils occurred. The plants were in a poor state of vigor and very weak and chlorotic. A few berries were set but these fell before reaching maturity and the vines were listed as being questionably staminate. Two staminate hybrid (*riparia*×*rupestris*) individuals used for rootstock purposes were observed to set a few berries from flowers which showed slight development of the pistils. However, these berries apparently were of parthenocarpic origin since only a few escaped falling before maturity and these were entirely seedless.

In the opinion of the writer the slight variation in the degree of development of the pistil in staminate flowers and the differences in the degree of reflexing of the stamens of pistillate-flowered forms are but mere variations in the phenotypic expression of the two sex forms and, as such, in no way represent intermediate or intersexual forms. There is no evidence of the transformation of the organs of one sex into those of the other sex.

Neither is there evidence of intergrading or intermediate degrees of sexual activity of either the male or female organs. The work of Kaczmarek (1938) in studying germination of pollen of several hundred individuals of which more than 170 were pistillate forms, gave no evidence of intermediate proportions of pollen germination. In all cases the percentage germination was either nil or high. Work done at this Station indicated similar behavior. On the strength of this information the author is convinced that the various degrees of recurving of the stamens of pistillate flowers in no way represent or condition the sexual response of those organs. While such slight variations in the stamens as well as those in the development of the pistils may be genetically determined, it is the belief of the author that the genes governing them are not the primary genes which control the fertility or the sterility of those sex organs.

Only two cases of pronounced floral abnormality were observed during the course of the study. Two seedling vines [Sheridan× (Manito×Delaware)] bore flowers which appeared to be normal hermaphrodites but which had very short erect stamens. The pistils of these flowers appeared to be somewhat compressed and showed several suture lines. The pistils were easily split along these lines and so disclosed another inner whorl of reduced stamens surrounding a much reduced pistil which again revealed distinct suture lines. These flowers set no fruit when bagged and only a few scattered berries when open to cross pollination. The berries set were apparently parthenocarpic since the few which matured were seedless. These flowers may be considered similar to the "pure female" flowers described by Baranov (1927b) tho in the flowers described by him the outer whorl of stamens was entirely lacking.

In general, the segregation of these three normal flower types was distinct and clearcut. In only a few cases was there reason to hesitate over the classification and these involved distinction between hermaphroditic and pistillate forms. These were instances in which young or weak vines bearing only a few small flower clusters escaped detection until they had passed the full bloom stage at which time the position of the stamens with reference to the pistil was difficult to establish. Staminate vines were always easy to detect by the greater size of the cluster, more showy appearance, pronounced fragrance, and the fact that they tended to bloom several days earlier than pistillate or hermaphroditic sister seedlings. The only questionable staminate plants observed were the two seedlings [(Keuka×Sultanina) and (Muscat Hamburg×Hubbard)], already described. Some clusters of flowers on these plants showed partially developed pistils, while other clusters appeared to have only typical staminate flowers. Since these plants set only a few parthenocarpic berries, tho open to cross pollination, they were listed temporarily as being questionably staminate. Both plants died during the winter subsequent to the season in which the observations were made so further observations on their floral behavior were impossible. In view of their low state of vigor, the author is of the opinion that the few flowers produced in 1937 were not normal and that the incomplete development of the pistils may have been caused by the poor condition of the plants.

On the basis of the foregoing observations the author has been convinced that in the grape one does not have to do with a dioecious condition resulting from an outright deficiency of floral organs but rather with an example of dioecism due to a suppression of the function of the organs of one or the other of the sexes of the true hermaphrodite. From this premise a different system of nomenclature is recommended. The objections to the application of the terms male and female have already been mentioned. The terms staminate and pistillate are not entirely correct since they imply that a given individual produces flowers with the organs of one sex only. For these reasons the writer suggests the application of the terms "male sterile" and "female sterile" to pistillate and staminate floral forms, respectively. However, in order to avoid undue confusion in the text of this discussion the terms "functionally staminate" and "functionally pistillate" will be applied to the forms which, in reality, are female sterile and male sterile forms of hermaphrodites, but with the proviso that they are merely being substituted for the more desirable ones. In the various tables presented in this paper the accepted genetic insignia for male, female, and hermaphroditic individuals will be substituted for the above terms for the sake of brevity.

The accompanying list of varieties, classified according to flower type, were used as parents in the crosses from which the data presented in the subsequent tables were derived.

FUNCTIONALLY HERMAPHRODITIC AMERICAN VARIETIES

Agawam
Beta
Big Hope
Berckmans
Brilliant
Brocton [Brighton × (Winchell × Diam.)]*
Campbell
Catawba
Champion
Clinton
Collier
Concord
Conc. Seedless (Hubbard Seedless)
Croton
Delaware
Diamond

---

*Indicates Station-bred variety.

Dunkirk (Brighton × Jefferson)*
Dutchess
Eden [Ontario × (Triumph × Mills)]*
Eumadel
Fredonia (Champion × Lucile)*
Goethe
Golden Muscat (Musc. Hamb. × Diamond)*
Governor Ross
Hanover (Brighton × Niagara)*
Hector (Chasselas Rose × Brocton)*
Helen Keller
Hidalgo
Hubbard
Hybrid Franc
Iona
Isabella
Jefferson
Kensington
Keuka (Chasselas Rose × Mills)*
Little Blue
Lucile

Lutie
Mills
Moore
Nectar
Niagara
Ontario (Winchell × Diamond)*
Portland (Champion × Lutie)*
Regal
Ripley (Winchell × Diamond)*
Rommel
Secretary
Seneca (Lignan Blanc × Ontario)*
Sheridan (Herbert × Worden)*
Stout Seedless [(Triumph × Dutch.) × Sultanina]*
Triumph
Urbana (Ross × Mills)*
Watkins (Mills × Ontario)*
Wayne (Mills × Ontario)*
Winchell
Worden
Yates (Mills × Ontario)*

---

*Indicates Station-bred variety.

FUNCTIONALLY PISTILLATE AMERICAN VARIETIES

Black Eagle
Brighton
Canandaigua
Delago
Eclipse
Herbert

Hercules
Lindley
Mead No. 9
Merrimac
Salem

FUNCTIONALLY HERMAPHRODITIC EUROPEAN VARIETIES

Black Corinth
Black Monukka
Csaba
Chablis
Chasselas Besson
Chasselas Ciotat
Chasselas Golden
Chasselas Rose
Chasselas Rose Violet

Franken Riesling
Gros Guillaume
Khalili
Lignan Blanc
Muscat Hamburg
Muscat St. Laurent
Sultana
Sultanina
White Corinth
Zinfandel

FUNCTIONALLY PISTILLATE EUROPEAN VARIETIES

Bakator

HERMAPHRODITIC STATION SEEDLINGS

No. 5 (Concord × V. *vulpina*)
No. 116 (Winchell × Diamond)
No. 123 (Winchell × Diamond)
No. 125 (Winchell × Diamond)
No. 154 (Agawam × *V. labrusca*)
No. 160 (Eumelan × Faith)
No. 673 (Agawam selfed)
No. 797 (Goff o.c.p.)
No. 818 (Goff o.c.p.)

No. 931 (Worden × Sta. 123)
No. 933 Worden × Sta. 123)
No. 934 (Worden × Sta. 123)
No. 939 (Ross × Mills)
No. 1231 (Aminia selfed)
No. 1233 (Aminia selfed)
No. 1289 (Brighton selfed)
No. 2717 (Brighton × Rochester)
No. 2801 (Herbert × Worden)

No. 2898 (Lindley × Niagara)
No. 2900 (Lindley × Niagara)
No. 2905 (Lindley × Niagara)
No. 2907 (Lindley × Worden)
No. 2917 (Lindley × Worden)
No. 3516 (Collier × Mills)
No. 3517 (Ross × Mills)
No. 3518 (Ross × Mills)
No. 3644 (Mills × Ross)
No. 4066 (Sta. 116 × Jefferson)
No. 4071 (Sta. 116 × Jefferson)
No. 4293 (Salem × Worden)
No. 4354 (Black Eagle × Mills)
No. 4486 (Ozark × Mabel)
No. 4560 (Herbert × Worden)
No. 4571 (Salem × Worden)
No. 4754 (Salem × Worden)
No. 7408 (Sta. 939 selfed)
No. 7588 (Mills × Ontario)
No. 7601 (Mills × Ontario)
No. 7917 (Diamond × Croton)
No. 7957 (Gaertner × Mills)
No. 7984 (Eldorado × Concord Seedless)
No. 8010 (Iona × Concord Seedless)
No. 8085 (Prentiss × Concord Seedless)
No. 8131 (Sta. 3517 × Winchell)
No. 8174 (Secretary × Campbell)
No. 8187 (Vergennes × Concord Seedless)
No. 8188 (Vergennes × Concord Seedless)
No. 8357 (Campbell × Triumph)
No. 8396 (Delaware × Goff)
No. 8457 (Franken Riesling × Diamond)
No. 8536 (Goff × Iona)
No. 8537 (Goff × Iona)
No. 8717 (Kensington × Triumph)
No. 8753 (Kensington × Concord Seedless)
No. 9130 (Triumph × Delaware)
No. 9135 Triumph × Dutchess)

No. 9202 (Campbell × Secretary)
No. 9226 (Chasselas Besson × Diana)
No. 9524 (Secretary × Campbell)
No. 9527 (Secretary × Campbell)
No. 9545 (Secretary × Campbell)
No. 9549 (Secretary × Campbell)
No. 9551 (Secretary × Campbell)
No. 9942 (Grosse Blanc × Mills)
No. 10085 (Triumph × Mills)
No. 10096 (Triumph × Mills)
No. 10104 (Triumph × Mills)
No. 10108 (Triumph × Mills)
No. 10115 (Triumph × Mills)
No. 10144 (Triumph × Mills)
No. 10346 Chasselas Golden × Collier)
No. 10358 Chasselas Golden × Collier)
No. 10392 (Muscat Hamburg × Collier)
No. 10410 (Muscat Hamburg × Collier)
No. 10420 (Muscat Hamburg × Collier)
No. 10526 (Muscat Hamburg × Croton)
No. 10606 (Frankenthal Precoce × Ripley)
No. 10608 (Frankenthal Precoce × Ripley)
No. 10774 (Chasselas Besson × Diana)
No. 10782 (Sta. 10144 × Diamond)
No. 10814 (Chasselas Ciotat × Mills)
No. 10902 (Sta. 8396 × Concord Seedless)
No. 10903 (Sta. 8396 × Concord Seedless
No. 10905 (Sta. 8396 × Concord Seedless)
No. 10919 (Sta. 9135 × Sultanina)
No. 10920 Sta. 9135 × Concord Seedless)
No. 11737 (Ontario × Sta. No. 10085)

FUNCTIONALLY PISTILLATE STATION SEEDLINGS

No. 4350 (Black Eagle × Mills)
No. 4491 (Ozark × Mabel)
No. 4570 (Salem × Worden)
No. 7576 (Mills × Ontario)
No. 7879 (Delago × Diamond)
No. 8243 (Black Eagle × Concord Seedless)
No. 8391 (Delago × Concord Seedless)

No. 8691 (Iona × Sta. 3459)
No. 9104 (Triumph × Iona)
No. 10436 (Bakator × Brocton)
No. 10438 (Bakator × Brocton)
No. 10439 (Bakator × Brocton)
No. 10605 (Frankenthal Precoce × Diamond)
No. 10842 (Herbert × Sta. 9135)

FUNCTIONALLY STAMINATE STATION SEEDLINGS

No. 146 (Winchell × *V. aestivalis*)

No. 156 (Agawam × *V. labrusca*)

Tables 1 and 2 present the distribution of floral types in the progenies derived from crosses involving some of the more important commercial varieties, Station-bred seedlings, and native species.

TABLE 1.—RESULTS OF CROSSES INVOLVING SOME OF THE MORE IMPORTANT COMMERCIAL VARIETIES OF GRAPES, SOME HYBRID SEEDLINGS AND PURE SPECIES.*

	Agawam	Brighton	Campbell	Chasselas Golden	Chasselas Rose	Concord	Delaware	Diamond	Dutchess	Eclipse	Franken Riesling	Fredonia	Golden Muscat	Herbert	Hercules	Hubbard	Kensington	Keuka	Lindley	Lucile	Merrimac	Mills	Moore	Muscat Hamburg	Ontario	Portland	Salem	Secretary	Seibel No. 2	Seneca	Sheridan	Triumph	Wayne	Winchell
Agawam	18 7 0																																	
Black Corinth		9 7 0											124 25 0		38 30 0			3 1 0							34 7 0									
Brighton		12 6 1																			2 2 0													
Campbell		2 3 0	4 1 0										193 48 0		0 1 0							0 1 0					1 1 0	49 0 0		23 0 0			8 1 0	
Catawba		0 1 0												19 9 0													2 0 0					5 6 0		
Concord				8 1 0	2 1 0	107 13 0				3 3 0								5 3 0						25 0 0										
Delaware		5 0 0	0 1 0				17 5 0		1 0 0		2 0 0											5 3 0		1 0 0								2 0 0		1 0 0
Diamond								19 4 0	1 0 0		3 0 0						12 0 0					11 3 0		10 0 0								5 0 0		26 4 0
Dutchess					12 3 0				5 0 0	25 3 0																						13 0 0		
Franken Riesling									5 0 0																				10 2 0					
Fredonia										5 8 0			23 8 0			14 11 0										5 3 0				5 0 0				
Golden Muscat										17 12 0						44 9 0															2 2 0			
Gros Guillaume																25 0 0									35 2 0									
Hercules															11 5 0																			
Hubbard				27 12 0	32 22 0		63 22 0								5 0 0	12 6 0	14 1 0					17 8 0		38 0 0	13 6 0	26 13 0								
Jefferson		30 26 0																																
Kensington																	3 0 0																	

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*The upper figure in the series derived from any cross represents the number of functionally hermaphroditic progeny, the second figure the number of functionally pistillate progeny, and the third figure the number of functionally staminate progeny.

TABLE 1—*Continued.*

	Agawam	Brighton	Campbell	Chasselas Golden	Chasselas Rose	Concord	Delaware	Diamond	Dutchess	Eclipse	Franken Riesling	Fredonia	Golden Muscat	Herbert	Hercules	Hubbard	Kensington	Keuka	Lindley	Lucile	Merrimac	Mills	Moore	Muscat Hamburg	Ontario	Portland	Salem	Secretary	Seibel No. 2	Seneca	Sheridan	Triumph	Wayne	Winchell
Lindley																					6 8 0													
Merrimac		2 4 0																			5 6 0													
Mills			3 0 0	4 1 0	9 2 0		0 1 0	2 2 0						1 2 0								1 0 0			3 1 0		1 2 1					42 14 0		
Moore													19 4 0										0 1 0		105 35 0									
Muscat Hamburg																21 0 0									2 0 0									
Ontario		16 17 0		1 3 0							18 16 0					11 5 0		9 5 0		31 19 0		3 5 0			31 9 0						36 8 0		26 8 0	
Panariti		3 9 0																29 7 0																
Portland		31 35 0		8 7 0						50 44 0						28 6 0							2 0 0	16 0 0	6 6 0									
Salem			1 0 0																		0 2 0	2 0 0												
Secretary			29 0 0																			1 0 0						2 0 0						
Seibel No. 2							4 1 0		22 0 0		60 13 0											1 0 0							38 11 0					
Seneca																															50 0 0			
Sheridan		20 13 0			5 1 0			4 0 0	2 0 0	2 3 0			68 19 0			1 3 0								1 0 0	41 13 0						59 26 0		38 15 0	
Stout Seedless													44 0 0					29 0 0																
Sultana													32 0 0		25 0 0			1 0 0																
Sultanina													14 13 0	32 12 0											36 11 0									
Triumph			20 4 0	4 2 0					2 0 0								5 0 0					5 3 0										10 1 0		

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*The upper figure in the series derived from any cross represents the number of functionally hermaphroditic progeny, the second figure the number of functionally pistillate progeny, and the third figure the number of functionally staminate progeny.

TABLE 1—*Continued.*

	Agawam	Brighton	Campbell	Chasselas Golden	Chasselas Rose	Concord	Delaware	Diamond	Dutchess	Eclipse	Franken Riesling	Fredonia	Golden Muscat	Herbert	Hercules	Hubbard	Kensington	Keuka	Lindley	Lucile	Merrimac	Mills	Moore	Muscat Hamburg	Ontario	Portland	Salem	Secretary	Seibel No. 2	Seneca	Sheridan	Triumph	Wayne	Winchell
Vergennes		6 11 0	2 3 0					1 1 0																										5 5 0
Vitis aestivalis																																		2 3 6
Vitis labrusca	2 2 1																																	
Vitis riparia						4 0 4																												
Watkins													33 9 0																	1 0 0				
Wayne													62 13 0											1 0 0									26 2 0	
Winchell			5 0 0					2 1 0									3 0 0																	14 1 0
Worden		2 1 0	6 4 0									38 7 0	35 25 0						29 34 0		26 29 0						33 39 0							
Zinfandel									4 3 0																6 0 0									
Sta. Seedling No. 5								22 11 0																										
Sta. Seedling No. 125		15 26 0																																
Sta. Seedling No. 146		2 0 2					2 0 2																											
Sta. Seedling No. 156		5 0 8																																9 0 12
Sta. Seedling No. 9549																		3 1 0															32 13 0	
Sta. Seedling No. 9976																									27 7 0									
Sta. Seedling No. 9978																									19 4 0									
Sta. Seedling No. 10085							22 10 0		7 3 0			23 8 0		37 12 0											5 4 0									

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*The upper figure in the series derived from any cross represents the number of functionally hermaphroditic progeny, the second figure the number of functionally pistillate progeny, and the third figure the number of functionally staminate progeny.

TABLE 1—*Concluded.*

	Agawam	Brighton	Campbell	Chasselas Golden	Chasselas Rose	Concord	Delaware	Diamond	Dutchess	Eclipse
Sta. Seedling No. 10104							21 10 0		4 0 0	
Sta. Seedling No. 10108									2 0 0	
Sta. Seedling No. 10115							51 0 0		4 0 0	
Sta. Seedling No. 10144										

	Franken Riesling	Fredonia	Golden Muscat	Herbert	Hercules	Hubbard	Kensington	Keuka	Lindley	Lucile	Merrimac	Mills	Moore	Muscat Hamburg
Sta. Seedling No. 10104														
Sta. Seedling No. 10108														
Sta. Seedling No. 10115														
Sta. Seedling No. 10144														

	Ontario	Portland	Salem	Secretary	Seibel No. 2	Seneca	Sheridan	Triumph	Wayne	Winchell
Sta. Seedling No. 10104										
Sta. Seedling No. 10108	5 3 0									
Sta. Seedling No. 10115										
Sta. Seedling No. 10144						5 0 0				

*The upper figure in the series derived from any cross represents the number of functionally hermaphroditic progeny, the second figure the number of functionally pistillate progeny, and the third figure the number of functionally staminate progeny.

DISCUSSION

Examination of the data in Tables 1 and 2 reveals several important features, as follows: (a) The majority of the functionally hermaphroditic varieties are not homozygous for that character for when self-fertilized or intercrossed they produce progeny including both hermaphrodites and functionally pistillate flowered types with a preponderance of hermaphrodites. (b) Some hermaphroditic varieties, e. g., Muscat Hamburg, Seneca, Sultana, etc., apparently are homozygous for functional hermaphroditism since all of their progeny are hermaphroditic regardless of whether the other parent of the cross is functionally pistillate or of the heterozygous hermaphroditic type. (c) In general, functionally staminate individuals appear only when the pollen parent of the cross is functionally staminate. (d) Functionally pistillate flowered individuals when pollinated by functional heterozygous hermaphrodites gives an approximation of half functionally staminate and half functionally pistillate progeny. When fertilized by homozygous functional hermaphrodites, all of the progeny are functional hermaphrodites. (e) Functionally pistillate individuals, tho essentially entirely self-sterile because of the inviable nature of their pollen, do very infrequently produce a few viable pollen grains, as is shown by the fact that a few viable seeds and seedlings are produced by selfing the flowers of such varieties. A few seedlings were produced also by using pollen from varieties having reflexed stamens on the pistils of other varieties having reflexed stamens and on the pistils of functionally hermaphroditic varieties. That these seedlings are not apomictic in origin is indicated by the segregations in flower types and other plant characters which were observed in the seedlings.

Analysis of the above facts suggests that the character of male sterility is the result of the action of recessive genes since male sterile forms appear in the progeny resulting from intercrossing certain of the functionally hermaphroditic varieties. The character of female sterility, on the other hand, appears to be a dominant one since it appears only if one (the male) of the parents has that character.

On the basis of these observations, the following genic explanation is suggested:

Sp = genic complex for normal pollen development.
sp = genic complex which inhibits normal pollen development.
So = genic complex which inhibits normal ovule development.
so = genic complex for normal ovule development.

Table 2.—Results of Crosses Involving Station-Bred Seedlings.*

Cross	No. 98	No. 116	No. 123	No. 797	No. 933	No. 934	No. 1231	No. 1233	No. 1289	No. 2900	No. 3516	No. 3518	No. 4570	No. 4574	No. 7408	No. 7576	No. 7917	No. 8536	No. 8537	No. 8691	No. 8717	No. 9104	No. 9145	No. 9202	No. 9527	No. 9545	No. 9549	No. 9551	No. 10358	No. 10392	No. 10410	No. 10420	No. 10436	No. 10438	No. 10439	No. 10526	No. 10605	No. 10606	No. 10774	No. 10782	No. 10814	No. 10842	No. 10919	No. 10920	No. 11737
Selfed.	10 0 0			10 8 0	34 0 0	20 0 0	15 2 0	48 10 0	9 4 0	18 2 0			8 6 0	60 30 0			13 1 0	1 0 0	1 0 0		5 0 0				11 1 0					3 0 0	1 0 0										5 1 0		4 0 0		9 2 0
Black Corinth																		26 0 0					16 1 0																					6 6 0	
Black Monukka																																											4 0 0		
Campbell															1 3 0																														
Catawba		1 2 0																																											
Diamond																		42 0 0			4 0 0																								
Goethe				7 1 0																																									
Golden Muscat																												3 0 0													0 3 0				15 4 0
Hubbard																1 2 0																						7 9 0							
Jefferson		7 3 0																																											
Khalili																				1 0 0		6 8 0										14 0 0				32 14 0									
Lutie		12 10 0																																											
Mills																			14 0 0																		12 6 0								
Moore															69 19 0												21 4 0																		
Muscat Hamburg																18 0 0				7 0 0	34 0 0												38 1 0						37 0 0	16 0 0					
Ontario															37 10 0			45 0 0	28 0 0								13 5 0		1 0 0					10 9 0			13 16 0	9 16 0							

---

*The upper figure in the series derived from any cross represents the number of functionally hermaphroditic progeny, the second figure represents the number of functionally pistillate progeny, and the lowest figure represents the number of functionally staminate progeny.

TABLE 2—*Concluded.*

Cross	No. 98	No. 116	No. 123	No. 797	No. 933	No. 934	No. 1231	No. 1233	No. 1289	No. 2900	No. 3516	No. 3518	No. 4570	No. 4574	No. 7408	No. 7576	No. 7917	No. 8536	No. 8537	No. 8691	No. 8717	No. 9104	No. 9145	No. 9262	No. 9527	No. 9545	No. 9549	No. 9551	No. 10358	No. 10392	No. 10410	No. 10420	No. 10436	No. 10438	No. 10439	No. 10526	No. 10605	No. 10606	No. 10774	No. 10782	No. 10814	No. 10842	No. 10919	No. 10920	No. 11737
Panariti																		9 1 0					22 7 0																					2 1 0	
Portland																																						2 3 0							
Secretary												11 0 0																																	
Seneca																5 0 0		16 0 0			8 0 0	21 0 0			10 0 0	11 1 0		6 0 0	20 0 0		49 0 0				12 0 0						8 0 0				31 0 0
Sheridan																	27 15 0	17 0 0					4 2 0												7 8 0										
Stout Seedless																		18 0 0					23 0 0																				6 0 0		
Sultana																																										51 0 0		7 0 0	
Sultanina																		59 0 0																								4 10 0		25 7 0	
Watkins															12 6 0	3 1 0		1 0 0									9 6 0																		
Wayne															12 2 0		5 7 0				13 0 0						6 0 0																		
Winchell												1 0 0									22 0 0																								
Franken Riesling											14 0 1																																		
Sta. No. 146			3 0 4																																										
Sta. No. 3517											1 0 0																																		
Sta. No. 9145																																				37 15 0									
Sta. No. 10919																		11 0 0																										3 0 0	

*The upper figure in the series derived from any cross represents the number of functionally hermaphroditic progeny, the second figure represents the number of functionally pistillate progeny, and the lowest figure represents the number of functionally staminate progeny.

Using the factors listed, the following genotypes may be set up:

$So\;so\;Sp\;sp$ = female sterile hermaphrodite or staminate type.

$so\;so\;sp\;sp$ = male sterile hermaphrodite or pistillate type.

$so\;so\;Sp\;sp$ = functional hermaphrodite.

Crossing a functionally staminate (female sterile) type with a functionally pistillate (male sterile) type should produce the following genotypes in the F_1 generation:

$$\overset{\text{♀}}{so\;so\;sp\;sp} \times \overset{\text{♂}}{So\;so\;Sp\;sp} = \begin{cases} \left.\begin{array}{l} 1\; so\;so\;sp\;sp = \text{pistillate (male sterile)} \\ 1\; So\;so\;Sp\;sp = \text{staminate (female sterile)} \end{array}\right\} \text{parental types} \\ 1\; so\;so\;Sp\;sp = \text{functional hermaphrodite} \\ 1\; So\;so\;sp\;sp = \text{sterile for both pollen and eggs} \end{cases}$$

However, from such crosses only the two parental types have ever been reported as having been obtained. The other two types have never been reported as resulting from this type of cross and the type of individual which is sterile for both pollen and egg has never been reported in grapes under any conditions whatever. Therefore, one may assume that either of these two types are obtained very rarely from the type of cross illustrated, if ever at all. To be sure, one must admit that the male-female sterile type might easily pass unnoticed and be mistakenly classified as a female sterile or staminate vine unless particular attention were paid to the character of its stamens. Moreover, since this form would be unable to reproduce itself, it would soon pass out of existence as the result of what may well be called a reproductive lethal character. However, since the functional hermaphrodite arising from the cross illustrated could participate as either, or both, the male or female parent, one should expect to find functionally hermaphroditic individuals becoming proportionately more numerous thru successive generations. Furthermore, such individuals, being self fertile, would not be dependent on proximity of functionally staminate vines in order to be fruitful and would be much more advantageously situated from the standpoint of continuing themselves than would either of the distinctly unisexual types. Therefore, the appearance in the past of only a few functional hermaphrodites in wild populations should have resulted in this type establishing itself. That situation decidedly has not been the case in the native state since only the male sterile (functionally pistillate) and female sterile (functionally staminate) forms have been definitely proved ever to occur in the wild state. From this premise one may well conclude that from crosses of male sterile by female sterile individuals only the two parental types are ever obtained.

The recovery of only the two parental types in the progeny of a dihybrid cross at once suggests association of factors. The two suppressor genes, So and sp, must be borne on the same chromosome; that is, these two factors are linked, indeed so closely linked in their inheritance that crossing-over between them never occurs. Then a cross of a male sterile (functionally pistillate) individual by a female sterile (functionally staminate) individual would give

$$\frac{so\;sp}{so\;sp} = \text{male sterile vine} \qquad \frac{So\;Sp}{so\;sp} = \text{female sterile vine}$$

$$\overset{\text{♀}}{\frac{so\;sp}{so\;sp}} \times \overset{\text{♂}}{\frac{So\;Sp}{so\;sp}} = 1\overset{\text{♀}}{\frac{so\;sp}{so\;sp}} : 1\overset{\text{♂}}{\frac{So\;Sp}{so\;sp}}.$$

This cross gives the expected 1:1 ratio of staminate to pistillate individuals found in a dioecious species. To be sure many authors have reported a preponderance of staminate forms among wild populations of grape vines, but a possible explanation for that circumstance will be suggested at a later stage of the discussion.

If a functionally pistillate vine is crossed with pollen from a functional hermaphrodite of the above genotype, the following results will be obtained: $\overset{\text{♀}}{\frac{so\;sp}{so\;sp}} \times \overset{\text{⚥}}{\frac{so\;Sp}{so\;sp}} = 1\overset{\text{♀}}{\frac{so\;sp}{so\;sp}} : 1\overset{\text{⚥}}{\frac{so\;Sp}{so\;sp}}.$

The ratio so obtained is a typical backcross ratio and agrees well with the ratios reported by several authors as being obtained from such crosses.

If functional hermaphrodites of the above genotypic constitution are selfed or intercrossed, the following F_1 progeny should be expected:

$$\overset{\text{⚥}}{\frac{so\;Sp}{so\;sp}} \times \overset{\text{⚥}}{\frac{so\;Sp}{so\;sp}} = \begin{cases} \left.\begin{array}{l} 1\,\frac{so\;Sp}{so\;Sp} = \text{functional hermaphrodite} \\ 2\,\frac{so\;Sp}{so\;sp} = \text{functional hermaphrodite} \end{array}\right\} 3\text{⚥} \\ 1\,\frac{so\;sp}{so\;sp} = \text{functional pistillate} \quad -1\text{♀} \end{cases}$$

Fertilizing a functional hermaphrodite of the genotype given with pollen from a functionally staminate plant would give three types of progeny, as follows:

$$\overset{\text{⚥}}{\frac{so\ Sp}{so\ sp}} \times \overset{\text{♂}}{\frac{So\ Sp}{so\ sp}} = \left\{\begin{array}{l} \left.\begin{array}{l} 1\,\dfrac{So\ Sp}{so\ Sp} = \text{functional staminate} \\ 1\,\dfrac{So\ Sp}{so\ sp} = \text{functional staminate} \end{array}\right\} 2\text{♂} \\ 1\,\dfrac{so\ Sp}{so\ sp} = \text{functional hermaphrodite—1⚥} \\ 1\,\dfrac{so\ sp}{so\ sp} = \text{functional pistillate—1♀} \end{array}\right.$$

Here again the expected results are in harmony with those reported by other workers who have obtained an excess of staminate forms as compared with the respective numbers of functional hermaphrodites and pistillate forms.

It will have been observed that in the progeny obtained thru selfing or interbreeding functional hermaphrodites, one-third of the functionally hermaphroditic offspring obtained are of a new genotype, *viz.*, $\frac{so\ Sp}{so\ Sp}$. It is clearly apparent that individuals of this genotype must breed true for functional hermaphroditism, as follows:

$$\overset{\text{⚥}}{\frac{so\ Sp}{so\ Sp}} \times \overset{\text{⚥}}{\frac{so\ Sp}{so\ Sp}} = \text{all}\ \overset{\text{⚥}}{\frac{so\ Sp}{so\ Sp}} = \text{functional hermaphrodites.}$$

Furthermore, when this genotype is crossed on either functionally hermaphroditic or pistillate individuals, only functional hermaphrodites should occur in the progeny, as follows:

$$\overset{\text{♀}}{\frac{so\ sp}{so\ sp}} \times \overset{\text{⚥}}{\frac{so\ Sp}{so\ Sp}} = \text{all}\ \overset{\text{⚥}}{\frac{so\ Sp}{so\ sp}} = \text{functional hermaphrodites.}$$

$$\overset{\text{⚥}}{\frac{so\ Sp}{so\ sp}} \times \overset{\text{⚥}}{\frac{so\ Sp}{so\ Sp}} = 1\,\overset{\text{⚥}}{\frac{so\ Sp}{so\ Sp}} : 1\,\overset{\text{⚥}}{\frac{so\ Sp}{so\ sp}}\ \text{both are functional hermaphrodites.}$$

This situation at once suggests the behavior of the varieties Muscat Hamburg, Seneca, and Sultana, as has already been noted. These varieties apparently are homozygous for normal development of both pollen and egg or, in other words, do not carry either of the two suppressor genes.

When this type of functional hermaphrodite is fertilized with pollen from a staminate vine, only two types of progeny should result, as follows:

$$\overset{\text{⚥}}{\frac{so\ Sp}{so\ Sp}} \times \overset{\text{♂}}{\frac{So\ Sp}{so\ sp}} = 1\,\overset{\text{♂}}{\frac{So\ Sp}{so\ Sp}} : 1\,\overset{\text{⚥}}{\frac{so\ Sp}{so\ sp}}.$$

One will have observed that the staminate form obtained from this cross, like one of the two obtained by fertilizing the heterozygous functional hermaphrodite with pollen from a functionally staminate vine, differs genotypically from the parental functionally staminate individual in that the parental genotype is heterozygous for *Sp*, the dominant allelomorph of *sp* the pollen suppressor gene, whereas the derived genotype is homozygous for the dominant allelomorph *Sp*. Such genotypes homozygous for *Sp* would probably be difficult to distinguish phenotypically from the heterozygous genotype, but obviously the breeding behavior would be different.

$$\overset{\text{♀}}{\frac{so\ sp}{so\ sp}} \times \overset{\text{♂}}{\frac{So\ Sp}{so\ Sp}} = 1\,\overset{\text{♂}}{\frac{So\ Sp}{so\ sp}} : 1\,\overset{\text{⚥}}{\frac{so\ Sp}{so\ sp}}$$

$$\overset{\text{⚥}}{\frac{so\ Sp}{so\ sp}} \times \overset{\text{♂}}{\frac{So\ Sp}{so\ Sp}} = \left\{\begin{array}{l} \left.\begin{array}{l} 1\,\dfrac{So\ Sp}{so\ Sp}\ \text{functionally staminate} \\ 1\,\dfrac{So\ Sp}{so\ sp}\ \text{functionally staminate} \end{array}\right\} 2\text{♂} \\ \left.\begin{array}{l} 1\,\dfrac{so\ Sp}{so\ Sp}\ \text{functionally hermaphroditic} \\ 1\,\dfrac{so\ Sp}{so\ sp}\ \text{functionally hermaphroditic} \end{array}\right\} 2\text{⚥} \end{array}\right.$$

$$\overset{\text{⚥}}{\frac{so\ Sp}{so\ Sp}} \times \overset{\text{♂}}{\frac{So\ Sp}{so\ Sp}} = \left\{\begin{array}{l} 1\,\dfrac{So\ Sp}{so\ Sp}\ \text{functionally staminate} \\ 1\,\dfrac{so\ Sp}{so\ Sp}\ \text{functionally hermaphroditic} \end{array}\right.$$

Pollen from staminate individuals of this type would give 1:1 ratios of functionally hermaphrodite to functionally staminate individuals instead of the 1:1:2 ratios demonstrated in crosses involving the ordinary type of functionally staminate vine.

Further mention of this type of functionally staminate individual is deferred to a later stage of this discussion.

Mention may well be made here of another theoretically possible type of functionally staminate plant. This type of individual would be homozygous for both *So* and *Sp*, $\frac{So\ Sp}{So\ Sp}$. To be sure such an individual could arise only thru the failure of complete inhibitory action by the dominant suppressor gene on the abortive eggs of a functionally staminate vine, thus permitting the development of functional eggs of the following genotype: *So Sp*. If such an egg were fertilized by an *So Sp* male gamete an individual of the following genotype would result, $\frac{So\ Sp}{So\ Sp}$. Obviously such an individual when used as a pollen source for a cross would give only functionally staminate progeny, as follows:

$$\overset{\text{♀}}{\frac{so\ sp}{so\ sp}} \times \overset{\text{♂}}{\frac{So\ Sp}{So\ Sp}} = \text{all } \overset{\text{♂}}{\frac{So\ Sp}{so\ sp}} \text{ functionally staminate.}$$

$$\overset{\text{⚥}}{\frac{so\ Sp}{so\ sp}} \times \overset{\text{♂}}{\frac{So\ Sp}{So\ Sp}} = 1\,\overset{\text{♂}}{\frac{So\ Sp}{so\ sp}} : 1\,\overset{\text{♂}}{\frac{So\ Sp}{so\ Sp}} \text{ both functionally staminate.}$$

$$\overset{\text{⚥}}{\frac{so\ Sp}{so\ Sp}} \times \overset{\text{♂}}{\frac{So\ Sp}{So\ Sp}} = \text{all } \overset{\text{♂}}{\frac{So\ Sp}{so\ Sp}} \text{ functionally staminate.}$$

It is of interest to note here that the homozygous hermaphrodite is dominant to the (homozygous recessive) pistillate type but is recessive to the hypothetical homozygous staminate type of individual.

The possibility of a functionally staminate vine ever bearing fruit containing viable seeds is rather problematical, since, to the author's knowledge, no such instance has ever been reported. However, Dorsey (1912), Munson (1909), Kobel (1933), and others have reported cases of male vines setting fruit, but no mention was made of the seed development in such fruit. There seems little reason to doubt, however, that on rare occasions viable pollen is formed in the anthers of individuals having reflexed stamens, and it appears to the author that it should be equally probable that an occasional egg in the pistils of a functionally staminate form may not only fail to abort but, also, may become fertilized and develop into a viable seed. Such a problematical homozygous functionally staminate individual probably would not differ phenotypically from the ordinary functionally staminate individuals and would probably pass unnoticed unless opportunity to observe its breeding behavior were available.

Gladwin (1937) reported using pollen from a staminate individual, Aramon×Rupestris Ganzin No. 1 which has been widely used as a rootstock, on Concord Seedless, Barry and Agawam. Good sized populations were grown from these crosses but only staminate progeny resulted. A search of the literature revealed no other reference to similar behavior. However, staminate parents are rarely used by breeders of bunch grapes. A more extensive use of staminate pollen in hybridization might produce additional examples of homozygous staminate vines. Though this author was unable to check upon the origin of this staminate rootstock it does not appear to have originated through self-pollination of a staminate individual in the manner described in the preceding paragraph. Germinal mutation of *so* to *So* in the maternal gamete with subsequent fertilization by an *So* staminate gamete may have been responsible for the production of this exceptional individual.

According to the plan outlined, the inheritance of floral types represents an example of simple Mendelian inheritance and the various crosses should give simple Mendelian ratios. However, in applying this scheme to the data presented in Tables 1 and 2 numerous exceptions at once became evident. Upon examination of the data several important features become apparent. One will observe that all of the progeny from crosses involving certain functionally hermaphroditic parents were also functionally hermaphroditic regardless of whether the other parent involved was functionally hermaphroditic or functionally pistillate. Muscat Hamburg, Seneca, and Sultana have already been mentioned as displaying such behavior. In addition to these the following named varieties and Station seedlings also possessed this characteristic:

Secretary (Muscat Hamburg×Clinton)
Kensington (Clinton×Buckland Sweetwater)
Gros Guillaume (*Vitis vinifera*)
Stout Seedless (Sta. No. 9145×Sultanina)
Sta. Seedling No. 8536 (Goff×Iona)
Sta. Seedling No. 8537 (Goff×Iona)
Sta. Seedling No. 8717 (Kensington×Triumph)
Sta. Seedling No. 10115 (Triumph×Mills)

Populations of considerable size were grown from crosses involving these individuals and in only a few exceptional cases did functionally pistillate flowers appear. Several other varieties and Station seedlings were suspected of being of this nature, but only small populations of seedlings were grown from their crosses and for that reason they are not included in the list of homozygous functional hermaphrodites.

If crosses involving only those varieties which have shown themselves to be heterozygous for the hermaphroditic condition are considered, many show close approximation to the calculated 3:1 ratios (Table 3).

TABLE 3.—PROPORTION OF FUNCTIONALLY HERMAPHRODITE AND FUNCTIONALLY PISTILLATE INDIVIDUALS ARISING FROM CROSSES OF FUNCTIONAL HERMAPHRODITES BY FUNCTIONAL HERMAPHRODITES.

CROSS	FUNCTIONALLY HERMAPHRODITE	FUNCTIONALLY PISTILLATE
Ontario×Moore Early	105	35
Hubbard×Delaware	63	22
Mills×Hubbard	24	8
Wayne×Iona	25	8
Triumph×Mills	42	14
Golden Muscat×Fredonia	23	8
Golden Muscat×Sheridan	68	19
Ontario×Sheridan	42	13
Portland×Moore Early	26	7
Ontario selfed	31	9

Yet other combinations of these parents gave ratios which vary widely from the calculated 3:1 ratios (Table 4).

TABLE 4.—PROPORTION OF FUNCTIONALLY HERMAPHRODITE AND FUNCTIONALLY PISTILLATE INDIVIDUALS ARISING FROM CROSSES OF FUNCTIONAL HERMAPHRODITES BY FUNCTIONAL HERMAPHRODITES.

CROSS	FUNCTIONALLY HERMAPHRODITE	FUNCTIONALLY PISTILLATE
Chasselas Rose×Hubbard	32	22
Concord selfed	107	13
Golden Muscat×Black Corinth	124	25
Golden Muscat×Campbell	193	48
Golden Muscat×Moore	19	4
Golden Muscat×Wayne	62	13
Golden Muscat×Sultanina	14	13
Golden Muscat×Worden	35	25
Seibel No. 2×Norton	24	15
Ontario×Hubbard	26	13
Melton×Black Corinth	16	1
Sheridan×Ontario	36	8
Wayne selfed	26	2
Sheridan selfed	38	15
Diamond selfed	19	4
Lucile×Ontario	31	19

Such variations are so irregular and so inconsistent as to direction that no scheme of Mendelian inheritance could be applied to any considerable part of the crosses.

In considering the crosses of functionally pistillate forms by heterozygous functional hermaphrodites, the ratio of functional hermaphrodites to functional pistillate forms approaches very closely the calculated 1:1 ratio (Table 5).

TABLE 5.—PROPORTION OF FUNCTIONALLY HERMAPHRODITE AND FUNCTIONALLY PISTILLATE INDIVIDUALS ARISING FROM CROSSES OF FUNCTIONALLY PISTILLATE BY FUNCTIONAL HERMAPHRODITES.

CROSS	FUNCTIONALLY HERMAPHRODITE	FUNCTIONALLY PISTILLATE
Brighton×Jefferson	30	26
Brighton×Ontario	16	17
Brighton×Portland	31	35
Brighton×Niagara	11	12
Eclipse×Ontario	18	16
Eclipse×Portland	50	44
Lindley×Worden	29	34
Merrimac×Worden	26	29
Salem×Worden	33	39

However, some variations from the expected occur even in these crosses (Table 6).

TABLE 6.—PROPORTION OF FUNCTIONALLY HERMAPHRODITE AND FUNCTIONALLY PISTILLATE INDIVIDUALS ARISING FROM CROSSES OF FUNCTIONALLY PISTILLATE BY FUNCTIONAL HERMAPHRODITES.

CROSS	FUNCTIONALLY HERMAPHRODITE	FUNCTIONALLY PISTILLATE	DEVIATION FROM 1:1
Brighton×Panariti	3	9	3 ±1.2
Brighton×Vergennes	6	11	2.5±1.4
Brighton×Sta. No. 125	15	26	6.5±2.1
Hercules×Black Corinth	38	30	4 ±2.8
Eclipse×Golden Muscat	17	12	2.5±1.8
Eclipse×Fredonia	5	8	1.5±1.2
Total	84	96	6.0±4.5

As has been mentioned, the deviations from the calculated 3:1 and 1:1 ratios extend in either direction. Calculation of the probable errors shows few of these deviations to be significant departures from a 1:1 ratio. In many cases the populations from the invididual crosses are too small to be of much significance. Beyond question the ratios of the floral forms as observed in the field are not natural ratios. The plants reaching the flowering stage have undergone numerous kinds of selection and in many cases represent only a small remnant of the population originally started with. Of the large number of seeds obtained from a given cross usually many fail to germinate and of those which do germinate many produce seedlings which are so weak that they fail to survive to transplanting to the nursery row. In the nursery row there is frequently a heavy mortality from winter injury, fungous diseases, chlorotic malfunctions, and the like. In a practical breeding program in which one of the prime objectives to be obtained is maximum resistance against low temperatures, disease, and insect attacks, naturally the plants would be exposed to as many hazards as possible in the seedling stage in order to eliminate many of the susceptible individuals before they are transplanted to the permanent vineyard. For these reasons distorted ratios may easily have resulted, tho it is hard to conceive of any differential viability factor being associated with any particular flower type. Table 7 illustrates the heavy mortality occurring among the progeny resulting from a few representative crosses selected at random.

TABLE 7.—SUMMARY OF SOME CROSSES SELECTED AT RANDOM, SHOWING THE HIGH MORTALITY AMONG THE PROGENY.

CROSS	YEAR OF CROSS	NO. OF BERRIES SET	NO. CLUSTERS	NO. OF SEEDS SET	NO. SEEDS GERMINATED	NO. SEEDLINGS	NO. SEEDLINGS TRANSPLANTED	NO. PLANTS FLOWERING	FLOWER TYPE		
									⚥	♀	♂
Niagara selfed	1892	398	10	1,113	237	237	143	22	18	4	0
Agawam selfed	1892	194	10	442	65	44	34	17	11	6	0
Brighton × Sta. No. 5	1901	239	5	522	328	268	22	16	4	12	0
Brighton × Jefferson	1921	. . .	5	186	84	84	39	39	23	16	0
Catawba × Diamond	1923	45	2	100	43	22	12	10	10	0	0
Chasselas Rose × Sheridan	1923	60	2	92	48	38	9	7	5	2	0
Concord selfed	1909	386	10	425	111	111	8	8	7	1	0
Diamond selfed	1921	. . .	5	211	163	113	18	12	11	1	0
Golden Muscat × Watkins	1929	. . .	3	62	62	53	42	42	33	9	0
Hubbard × Gros Guillaume	1926	. . .	4	186	141	130	25	25	25	0	0

Since the populations of the individual crosses are so small, it seemed advisable to combine the populations of the more important varieties when crossed by other varieties. The results so obtained are presented in Table 8.

Grouping the data in this fashion shows to a better advantage the behavior of the different varieties when used as parents.

TABLE 8.—TABULAR SUMMATION OF THE PROGENY OF VARIETIES OF GRAPES AS INFLUENCED BY THE FLORAL TYPES OF THE OTHER PARENT.*

FEMALE PARENT	POLLINATED BY SELF	POLLINATED BY ⚥	POLLINATED BY ♀	POLLINATED BY ♂	POLLEN USED ON ⚥	POLLEN USED ON ♀
Agawam	18 7 0			4 0 1		
Brighton	12 6 1	203 216 1	2 6 0	7 0 10		2 2 0
Campbell	4 1 0	81 14 0	1 1 0		274 51 0	4 10 0
Catawba	5 12 0	24 6 0			6 8 0	26 17 0
Champion	16 6 0	32 10 0				
Chasselas Golden		115 48 0				
Chasselas Rose	5 0 0	72 34 0				
Clinton	15 3 0	2 1 0	2 0 0		12 10 0	
Concord	107 13 0	94 31 0		5 0 3	57 7 0	3 3 0
Delaware	17 5 0	94 34 0	1 0 0	4 0 2	29 13 0	5 0 0
Diamond	18 4 0	70 22 0			165 21 0	7 14 0
Dutchess	5 0 0	33 1 0			39 8 0	25 3 0
Eclipse	1 2 0	142 107 0				

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*The upper number in a series represents the hermaphroditic, the second represents the pistillate, and the third the staminate progeny.

TABLE 8—*Continued.*

FEMALE PARENT	POLLINATED BY SELF	POLLINATED BY ⚥	POLLINATED BY ♀	POLLINATED BY ♂	POLLEN USED ON ⚥	POLLEN USED ON ♀
Franken Riesling		73 15 0			75 5 1	
Fredonia		61 15 0			60 22 0	5 8 0
Golden Muscat		647 151 0			64 18 0	22 14 0
Herbert		66 46 0				
Hercules	11 5 0	74 35 0				
Hubbard	12 6 0	144 34 0			376 120 0	
Hybrid Franc	14 7 0	45 27 0			13 6 0	
Iona	1 4 0	49 18 0		1 0 0	48 25 0	1 1 0
Jefferson		15 7 0			11 3 0	30 26 0
Kensington	3 0 0	43 2 0				
Keuka		110 31 0			15 4 0	
Lindley		42 50 0				6 8 0
Lucile	2 1 0	31 19 0			5 2 0	11 6 0

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*The upper number in a series represents the hermaphroditic, the second represents the pistillate, and the third the staminate progeny.

TABLE 8—*Continued.*

FEMALE PARENT	POLLINATED BY SELF	POLLINATED BY ⚥	POLLINATED BY ♀	POLLINATED BY ♂	POLLEN USED ON ⚥	POLLEN USED ON ♀
Mead No. 9		28 25 0				
Melton		85 16 0				
Merrimac	5 6 0	26 29 0	8 12 0			2 4 0
Mills	1 0 0	94 28 0			71 27 0	27 22 0
Moore	0 1 0	29 8 0			274 69 0	
Muscat Hamburg		150 0 0			81 0 0	73 1 0
Ontario	31 9 0	386 108 0			320 97 0	68 74 0
Portland	1 0 0	59 24 0			73 22 0	89 94 0
Regal	41 7 0	18 10 0			4 2 0	
Salem		44 45 0			2 0 0	1 2 0
Secretary	2 0 0	78 0 0			32 0 0	2 0 0
Seibel No. 2	38 11 0	56 24 0			104 25 0	
Seneca		34 0 0			250 1 0	38 0 0

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*The upper number in a series represents the hermaphroditic, the second represents the pistillate, and the third the staminate progeny.

TABLE 8—*Continued.*

FEMALE PARENT	POLLINATED BY SELF	POLLINATED BY ⚥	POLLINATED BY ♀	POLLINATED BY ♂	POLLEN USED ON ⚥	POLLEN USED ON ♀
Sheridan	59 26 0	117 17 0			210 59 0	32 24 0
Stout Seedless					138 0 0	
Triumph	10 1 0	104 38 0	1 0 0		43 10 0	1 1 0
Watkins		16 3 0			68 21 0	
Wayne	26 1 0	135 48 0			127 31 0	
Winchell	14 1 0	45 13 0		11 0 18	27 7 0	
Worden					44 11 0	120 125 0
Black Corinth					226 40 0	54 44 0
Black Monukka					29 7 0	
Gros Guillaume					61 2 0	
Khalili					47 14 0	7 9 0
Sultana					65 0 0	51 0 0
Sultanina					243 60 1	7 19 0

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*The upper number in a series represents the hermaphroditic, the second represents the pistillate, and the third the staminate progeny.

TABLE 8—*Concluded.*

FEMALE PARENT	POLLINATED BY SELF	POLLINATED BY ⚥	POLLINATED BY ♀	POLLINATED BY ♂	POLLEN USED ON ⚥	POLLEN USED ON ♀
Bakator		25 37 0				
Sta. No. 7408	8 1 0	131 40 0			31 8 0	
Sta. No. 8536	1 0 0	244 1 0				
Sta. No. 8537	1 0 0	52 0 0				
Sta. No. 8717	5 0 0	82 0 0				
Sta. No. 10085		11 3 0			113 38 0	
Sta. No. 10115		9 0 0			57 1 0	18 0 0

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*The upper number in a series represents the hermaphroditic, the second represents the pistillate, and the third the staminate progeny.

The results in Table 8 are in error, however, because in grouping the data no heed was paid to the fact that certain of the functional hermaphrodites are homozygous for that character as has already been pointed out. The progeny of the homozygous functional hermaphrodites, as well as the crosses involving such parents, should receive separate grouping from those of the heterozygous functional hermaphrodites.

For that reason, the same data in Table 8 are presented in a revised form in Table 9. In the latter table the heterozygous and homozygous functional hermaphrodites are given separate treatment both when used as pollen parent and when used as the female parent. Inspection of the table shows that in many crosses the deviations from the expectancies are materially reduced.

TABLE 9.—TABULAR SUMMATION OF THE PROGENY OF THE MORE IMPORTANT VARIETIES SHOWING THE INFLUENCE OF THE FLORAL FORM AND BREEDING BEHAVIOR OF THE OTHER PARENT.*

Female parent	Pollinated by self	Pollinated by heterozygous ⚥	Pollinated by homozygous ⚥	Pollinated by ♀	Pollinated by ♂	Pollen used on heterozygous ⚥	Pollen used on homozygous ⚥	Pollen used on ♀
Agawam	18 7 0				4 0 1			
Brighton	12 6 1	185 216 1	18 0 0	2 6 0	7 0 10			2 2 0
Campbell	4 1 0	52 14 0	29 0 0	1 1 0		202 51 0	72 0 0	4 10 0
Catawba	5 12 0	24 6 0				6 8 0		26 17 0
Champion	16 6 0	32 10 0						
Chasselas Golden		115 48 0						
Chasselas Rose	5 0 0	89 34 0						
Clinton	15 3 0	2 1 0		2 0 0		12 10 0		
Concord	107 13 0	43 20 0	51 0 0		5 0 3	24 7 0	33 0 0	3 3 0
Delaware	17 5 0	94 34 0		1 0 0	4 0 0	28 13 0	1 0 0	5 0 0
Diamond	18 4 0	66 22 0	4 0 0			107 21 0	58 0 0	17 14 0

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*The upper number in any series represents the number of hermaphroditic, the second the number of pistillate, and the third the number of staminate progeny.

†Listed as reflexed one year and as hermaphroditic the next.

‡Listed as questionably staminate in 1937 until further observation.

TABLE 9.—*Continued.*

Female parent	Pollinated by self	Pollinated by heterozygous ⚥	Pollinated by homozygous ⚥	Pollinated by ♀	Pollinated by ♂	Pollen used on heterozygous ⚥	Pollen used on homozygous ⚥	Pollen used on ♀
Dutchess	5 0 0	33 1 0				38 8 0	1 0 0	25 3 0
Eclipse	1 2 0	142 107 0						
Franken Riesling		73 15 0				45 5 1	30 0 0	
Fredonia		61 15 0				55 22 0	5 0 0	5 8 0
Golden Muscat		571 151 0	76 0 0			64 18 0		22 14 0
Herbert		66 46 0						
Hercules	11 5 0	49 35 0	25 0 0					
Hubbard	12 6 0	98 34 0	46 0 0			338 120 0	38 0 0	10 12 0
Hybrid Franc	14 7 0	45 27 0				13 6 0		
Iona	1 4 0	49 18 0			1 0 0	48 25 0		1 1 0
Jefferson		15 7 0				11 3 0		30 26 0
Kensington	3 0 0	43 2 0						

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*The upper number in any series represents the number of hermaphroditic, the second the number of pistillate, and the third the number of staminate progeny.

†Listed as reflexed one year and as hermaphroditic the next.

‡Listed as questionably staminate in 1937 until further observation.

TABLE 9.—*Continued.*

Female parent	Pollinated by self	Pollinated by heterozygous ⚥	Pollinated by homozygous ⚥	Pollinated by ♀	Pollinated by ♂	Pollen used on heterozygous ⚥	Pollen used on homozygous ⚥	Pollen used on ♀
Keuka		110 31 0				15 4 0		
Lindley		42 50 0						
Mead No. 9		28 25 0						
Melton		67 18 0	18 0 0			37 18 0		
Merrimac	5 6 0	26 29 0		8 12 0				2 4 0
Mills	1 0 0	93 28 0	1 0 0			71 27 0		27 22 0
Moore	0 1 0	29 8 0				240 69 0	34 0 0	
Muscat Hamburg		150 0 0	‡			81 0 0		73 1 0
Ontario	31 9 0	349 106 0	37 2 0			236 97 0	84 0 0	68 74 0
Portland	1 0 0	59 24 0				57 22 0	16 0 0	89 94 0
Regal	41 7 0	18 10 0				4 2 0		
Salem		44 45 0				2 0 0		1 2 0

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*The upper number in any series represents the number of hermaphroditic, the second the number of pistillate, and the third the number of staminate progeny.

†Listed as reflexed one year and as hermaphroditic the next.

‡Listed as questionably staminate in 1937 until further observation.

TABLE 9—*Continued.*

Female parent	Pollinated by self	Pollinated by heterozygous ⚥	Pollinated by homozygous ⚥	Pollinated by ♀	Pollinated by ♂	Pollen used on heterozygous ⚥	Pollen used on homozygous ⚥	Pollen used on ♀
Secretary	2 0 0	78 0 0				32 0 0		2 0 0
Seibel No. 2	38 11 0	56 24 0				88 22 0	22 1* 0	
Seneca	29 0 0	5 0 0				226 1† 0	24 0 0	38 0 0
Sheridan	59 26 0	67 16 0	50 0 0			190 59 0	20 0 0	32 24 0
Stout Seedless						104 0 0	34 0 0	
Triumph	10 1 0	91 38 0	13 0 0	1 0 0		37 10 0	6 0 0	1 1 0
Watkins		16 3 0				54 21 0	14 0 0	
Wayne	26 1 0	135 48 0				95 31 0	32 0 0	
Winchell	14 1 0	45 13 0			11 3 18	27 7 0		
Worden						44 11 0		120 125 0
Black Corinth						187 40 0	39 0 0	54 44 0
Black Monukka						29 7 0		

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*The upper number in any series represents the number of hermaphroditic, the second the number of pistillate, and the third the number of staminate progeny.

†Listed as reflexed one year and as hermaphroditic the next.

‡Listed as questionably staminate in 1937 until further observation.

TABLE 9.—*Concluded.*

FEMALE PARENT	POLLINATED BY SELF	POLLINATED BY HETEROZYGOUS ⚥	POLLINATED BY HOMOZYGOUS ⚥	POLLINATED BY ♀	POLLINATED BY ♂	POLLEN USED ON HETEROZYGOUS ⚥	POLLEN USED ON HOMOZYGOUS ⚥	POLLEN USED ON ♀
Gros Guillaume						60 2 0		
Khalili						47 14 0		7 9 0
Sultana						65 0 0		51 0 0
Sultanina						170 59 1†	73 1 0	7 19 0
Bakator		27 37 0						
Sta. No. 7408	8 1 0	131 40 0				31 8 0		
Sta. No. 8536	1 0 0	210 1 0	34 0 0					
Sta. No. 8537	1 0 0	42 0 0						
Sta. No. 8717	5 0 0	74 0 0	8 0 0					
Sta. No. 10085		11 3 0				113 38 0		
Sta. No. 10115		9 0 0				56 1 0		18 0 0

*The upper number in any series represents the number of hermaphroditic, the second the number of pistillate, and the third the number of staminate progeny.

†Listed as reflexed one year and as hermaphroditic the next.

‡Listed as questionably staminate in 1937 until further observation.

TABLE 10.—A TABULAR SUMMATION FOR THE DATA IN TABLE 9 IN WHICH THE PROGENY OF THE VARIETAL CROSSES ARE GROUPED ACCORDING TO THE FLORAL FORM AND GENOTYPE OF THE PARENTAL FORMS.

FLORAL FORMS INVOLVED IN CROSS	OBSERVED PROGENY			CALCULATED PROGENY		
	⚥	♀	♂	⚥	♀	♂
Heterozygous ⚥ selfed	471	128	0	450	149	0
Homozygous ⚥ selfed	9	0	0	all	...	...
Heterozygous ⚥ × heterozygous ⚥	2,813	884	0	2,772	924	...
♀ × heterozygous ⚥	608	590	1	599	599	0
Homozygous ⚥ × heterzygous ⚥	635	3	0	all	...	...
Heterozygous ⚥ × homozygous ⚥	325	2	0	all	...	...
♀ × homozygous ⚥	43	0	0	all	...	...
Homozygous ⚥ × homozygous ⚥	47	0	0	all	...	...
Heterozygous ⚥ × ♀	7	1	0	....	...	...
Heterozygous ⚥ × ♂	25	3	24	....	...	...
♀ × ♂	7	0	10	....	...	...
Heterozygous ⚥ × heterozygous ⚥	2,762	882	2	2,733	911	0
Heterozygous ⚥ × homozygous ⚥	598	1	0	all	...	...
Homozygous ⚥ × heterozygous ⚥	578	2	0	all	...	...
♀ × heterozygous ⚥	566	484	0	525	525	0
♀ × homozygous ⚥	182	1	0	all	...	...
♀ selfed	5	8	0	0	0	0

Comparison of the observed and calculated frequencies (where the latter could be determined) in Table 10 shows very close agreement. The expected ratios from crosses involving pollen from functionally pistillate and functionally staminate plants could not be calculated. As has already been pointed out, it is theoretically possible for functionally staminate individuals of two genotypes to occur. These genotypes are as follows:

$\frac{So\ Sp}{so\ sp}$ = the original or native type of staminate plant.

$\frac{So\ Sp}{so\ Sp}$ = the derived type of staminate plant resulting from hybridizing functional hermaphrodites with staminate pollen.

In the early breeding work with grapes done at this Station several crosses were made involving cultivated functionally hermaphroditic and wild functionally staminate individuals. From such crosses two functionally staminate individuals were selected and used in further breeding work. These individuals were Station seedling No. 146 (Winchell × *V. aestivalis*) and Station seedling No. 156 (Agawam × *V. labrusca*). These two individuals were crossed on three cultivated varieties and on one seedling vine with the results shown in Table 11.

The results of the crosses illustrated in Table 11, tho the populations are small, indicate that the two functionally staminate pedi-

TABLE 11.—RESULTS OF CROSSES OF STATION SEEDLINGS NOS. 146 AND 156 ON FUNCTIONAL HERMAPHRODITES AND FUNCTIONALLY PISTILLATE FORMS.

CROSS	FLOWER FORM OF PROGENY		
	⚥	♀	♂
Brighton × No. 146	2	0	2
Brighton × No. 156	5	0	8
Delaware × No. 146	2	0	2
Winchell × No. 156	9	0	12
Sta. No. 123 (Winchell × Diamond) × No. 146	3	0	4
Total	21	0	28

greed seedlings are probably derived seedlings of the genotype $\frac{So\ Sp}{so\ Sp}$; that is, they are homozygous for the dominant gene *Sp* or for normal pollen development. However, some wild functionally staminate plants were also used in some crosses and therefore it hardly seems advisable to predict ratios for crosses involving such parents.

Likewise, it was not possible to predict ratios for progeny resulting from the use of pollen from fuctionally pistillate forms. In the opinion of the author the rare occurrence of viable pollen grains in the anthers of such plants is probably the result of spontaneous germinal mutations or possibly of chromosomal abberations, and as such produce unpredictable ratios in the resulting offspring.

No explanation is offered for the rare occurrence of exceptional functionally staminate or pistillate forms appearing in progeny where none would be expected on the basis of the Mendelian scheme presented in this discussion. Such exceptional forms may have been the result of pollen contamination, of clerical errors in numbering, or of germinal mutations.

Careful study of the results shown in Table 10 reveals that in every case in which numerical ratios could be calculated, the observed number of functional hermaphrodites was in excess of the calculated number, or conversely, the observed number of functionally pistillate individuals was deficient as compared to the calculated number. It will be remembered that numerous observations by other workers have indicated that in the wild state a predominance of functionally staminate over functionally pistillate forms exists. The similarity in the deficiency of functionally pistillate forms appearing in the types of crosses illustrated suggests that there may be a differential viability factor which is more or less closely associated with the functionally pistillate condition.

One may well speculate here as to the probable origin of the dioecious condition so nearly universally present in Vitis as it grows in its native state. Botanists and plant morphologists are generally of the opinion that dioecism is a phylogenetically younger condition than is functional hermaphroditism. The latter condition is considered to have been the original or primitive one in flowering plants and dioecism is thought to have arisen from hermaphroditism thru the loss or sterilization of one or the other of the sexual organs present in the primitive flower. The change from functional hermaphroditism to dioecism is considered to have occurred fairly recently from a geological standpoint. If the foregoing statements are accepted one may assume the original hermaphroditic floral condition in the grape to have been of the following genotype—$\frac{so\ Sp}{so\ Sp}$.

$$\overset{⚥}{\frac{so\ Sp}{so\ Sp}} \times \overset{⚥}{\frac{so\ Sp}{so\ Sp}} = \text{all } \overset{⚥}{\frac{so\ Sp}{so\ Sp}}$$

Then a dominant mutation occurred which affected the flower form by suppressing the development of the ovules and pistils: *so* (normal ovule development) → *So* (suppressed development of ovules).

In this way functionally staminate forms appeared: $\frac{So\ Sp}{so\ Sp}$ = staminate.

$$\overset{⚥}{\frac{so\ Sp}{so\ Sp}} \times \overset{♂}{\frac{So\ Sp}{so\ Sp}} = 1\ \overset{♂}{\frac{So\ Sp}{so\ Sp}} : 1\ \overset{⚥}{\frac{so\ Sp}{so\ Sp}}$$

The appearance of the functionally staminate form was then followed, or perhaps accompanied or even preceded, by a recessive mutation which affected the floral morphology and function by suppressing the normal development of the pollen: *Sp* (normal pollen development) →*sp* (suppressed pollen.)

$\frac{so\ Sp}{so\ sp}$ = functional hermaphrodite but heterozygous for the recessive pollen sterility gene.

Then the chance fertilization of such a heterzygous functional hermaphrodite by pollen from a functionally staminate vine would give two kinds of functional hermaphrodites and two kinds of functionally staminate individuals, as follows:

$$\overset{☿}{\frac{so\ Sp}{so\ sp}} \times \overset{♂}{\frac{So\ Sp}{so\ Sp}} = \begin{cases} 1\ \dfrac{So\ Sp}{so\ Sp}\ \text{staminate homozygous for normal pollen} \\ 1\ \dfrac{So\ Sp}{so\ sp}\ \text{staminate heterozygous for normal pollen} \\ 1\ \dfrac{so\ Sp}{so\ Sp}\ \text{hermaphrodite homozygous for normal pollen} \\ 1\ \dfrac{so\ Sp}{so\ sp}\ \text{hermaphrodite heterozygous for normal pollen} \end{cases}$$

Then chance fertilization of a heterozygous functional hermaphrodite with pollen from a heterozygous functionally staminate individual would give, in addition to functional hermaphrodites and functionally staminate individuals, plants bearing flowers of a new type—the functionally pistillate form, as follows:

$$\overset{☿}{\frac{so\ Sp}{so\ sp}} \times \overset{♂}{\frac{So\ Sp}{so\ sp}} = \begin{cases} 1\ \dfrac{So\ Sp}{so\ Sp}\ \text{homozygous functional staminate} \\ 1\ \dfrac{So\ Sp}{so\ sp}\ \text{heterozygous functional staminate} \\ 1\ \dfrac{so\ sp}{so\ sp}\ \text{functionally pistillate} \\ 1\ \dfrac{so\ Sp}{so\ sp}\ \text{heterozygous functional hermaphrodite} \end{cases}$$

The functionally pistillate form might have originated also through self fertilization of the heterozygous hermaphrodite as has been previously illustrated.

The functionally pistillate form when crossed by the heterzygous functional staminate breeds true for dioecism as has already been shown,

$$\overset{♀}{\frac{so\ sp}{so\ sp}} \times \overset{♂}{\frac{So\ Sp}{so\ sp}} = 1\,\overset{♂}{\frac{So\ Sp}{so\ sp}} : 1\,\overset{♀}{\frac{so\ sp}{so\ sp}}$$

The homozygous functionally staminate individuals and the functional hermaphrodites are assumed to have been less well suited to existing environmental conditions of that period and as a result were not able to meet the competition offered by the strictly dioecious forms. As a result the former mentioned types, along with the original

functional hermaphrodites, were gradually superseded by the forms breeding true for dioecism. However, some small remnant of functionally hermaphroditic stock must have survived and become the foundation of the cultivated functionally hermaphroditic grapes of today. However, since the latter type is not known to occur in the wild state anywhere in the world today, it is equally plausible that the functional hermaphrodite of cultivation may have appeared as the result of loss or mutation of one or the other of the suppressor genes. For example, the mutation of *sp* to *Sp* would change a functionally pistillate form, $\frac{so\ sp}{so\ sp}$, into a functional hermaphrodite, $\frac{so\ Sp}{so\ sp}$. Then, thru the proper crosses, all of the other genotypes discussed could appear. Similarly, the mutation of the dominant suppressor gene *So* to the recessive normal condition would transform a functionally staminate form, $\frac{So\ Sp}{so\ sp}$, into a functional hermaphrodite, $\frac{so\ Sp}{so\ sp}$. This hypothesis could easily explain the spontaneous appearance of the functionally hermaphroditic specimens of *Vitis rotundifolia* described by Reimer and Detjen (1910) and by Dearing (1917). Darrow (1937) recites, ". . . unknown Indians of Chile, South America, long before Columbus landed at San Salvador, had selected from among the wild strawberries that grew only along the beaches, plants that bore fruit of exceptional size . . . More important, however, the selected plants, or at least one of them, had perfect flowers, while all the true wild beach strawberries and most of the wild meadow strawberries of North America have the sexes borne on separate plants. Just how the Indians found such a perfect flowered plant, or how it came into cultivation must ever remain a mystery. An extensive search on the beaches of California, Washington and Oregon has failed to locate a single perfect flowered plant." The origin of the functionally hermaphroditic cultivated grape of today, like that of the perfect-flowered strawberry, still remains unsolved.

The system of sex inheritance in the grape, if one may lapse into the use of an undesirable term, as presented in the foregoing discussion, recognizes a distinction between sex potency and sex tendency. This distinction was emphasized by Correns (1928) and by Kobel (1929b). Every grape plant is considered to bear definite potencies for both maleness and femaleness in that its flowers bear organs whose functions are the production of male and female gametophytes.

Sex expression in the grape is influenced, as it is in other individuals, by genetic factors—probably many genetic factors. As has been pointed out by Allen (1932), environmental factors likewise produce effects which are parallel to those of the sex-influencing factors but which are never anything of the order of the sex potency factors. The latter endow the plant with both sets of sexual possibilities and the possibilities remain unchanged, however their expression may be encouraged or discouraged by other factors, either genetic or external.

The occurrence of mutations in some other of the many genetic factors controlling sex may be responsible for the rare occurrence of unexpected types from certain crosses and for the individuals described by Kobel as intersexes. Beadle (1932) has listed 15 separate and distinct genes for male sterility in maize and its seems reasonable to believe that genes for male or female sterility, other than the ones hypothesized by the author, may exist in the grape. Tests for allelomorphism of sterility factors are difficult to carry out with long-lived dioecious plants and until such studies are made the question as to whether such nonallelomorphic genes for sex sterility in grapes exist must remain open.

The scheme of heredity as suggested is not entirely dissimilar to that used by Jones (1932, 1934) in explaining the synthesis of a strain of maize which breeds true for dioecism. He made many crosses using tassel seed plants as the female parent and silkless plants heterozygous for tassel seed as the male parent. Of 41 progeny grown from these matings, 5 were found to give only two types of plants, functionally male and female. Therefore, those five families were entirely dioecious, the female parent giving only seed and the male parent only pollen. The crosses are represented as follows: ts_2 = gene for tassel seed which suppresses anthers in tassel and permits the latent female organ to develop. sk = gene for silkless which inhibits the pistillate flowers in the ear from developing.

$$sk\ sk\ ts_2\ ts_2 \times sk\ sk\ Ts_2\ ts_2 = \begin{cases} 1\ sk\ sk\ ts_2\ ts_2\text{—functionally female} \\ 1\ sk\ sk\ Ts_2\ ts_2\text{—functionally male} \end{cases}$$

Hence, Ts_2 is the only differential factor involved and the chromosome bearing it (No. 1) may be considered the sex chromosome in this family. However, as Jones points out, this sex mechanism is directly dependent upon the gene for silkless, sk, which is located on another chromosome (No. II), for its proper functioning. The silkless gene is considered to be a specifically male-promoting gene, supressing female tendencies. The tassel seed gene is distinctly a female-promoting gene. Thru their activity the organs of the opposite sex in either inflorescence, which have been dormant, are forced into development. The sterilizing effect of the silkless gene on the pistillate flowers in the tassel is entirely suppressed when both sk and ts_2 are present. However, in addition to these two genes, Jones considers that in maize there are many other genes working with physiological modifiers, both internal and external, which influence the development of the sex organs and bring about varying degrees of intergradation between the two sexes. These genes are considered to be complex in their action and widely distributed in the chromosomes.

Emerson (1932) synthesized two types of dioecism in maize in one of which the female plant is homogametic and the male plant heterogametic. This type involves the gene ts_2 for tassel seed and the gene ba_1 for barren stalk. This strain corresponds to the silkless-tassel seed dioecious strain improvised by Jones as follows:

$$\overset{\text{♀}}{ts_2ts_2\ ba_1ba_1} \times \overset{\text{♂}}{Ts_2ts_2\ ba_1ba_1} = 1\ \overset{\text{♀}}{ts_2ts_2\ ba_1ba_1} : 1\ \overset{\text{♂}}{Ts_2ts_2\ ba_1ba_1}.$$

In the other type synthesized by Emerson the female is heterogametic and the male homogametic. This was accomplished by substituting the dominant tassel-seed gene Ts_3 for the recessive ts_2.

$$\overset{\text{♀}}{Ts_3ts_3\ ba_1ba_1} \times \overset{\text{♂}}{ts_3ts_3\ ba_1ba_1} = 1\ \overset{\text{♀}}{Ts_3ts_3\ ba_1ba_1} : 1\ \overset{\text{♂}}{ts_3ts_3\ ba_1ba_1}$$

Under this setup the dominant Ts_3 gene controls the production of seed in the tassel of the female plant. The two types of dioecism in maize are possible because of the fact that the monoecism normally existing in that plant is the result of factors which bring about the suppression of the flowers of one sex in one inflorescence and of the flowers of the other sex in the other inflorescence of the plant. Suppression of the flowers usually appearing in a given inflorescence by certain genetic factors permits the development of the suppressed or latent flowers of the opposite sex which are also present in the same inflorescence.

The hypothesis accounting for dioecism in grapes as presented in this discussion assumes the female to be homozygous for two recessive pairs of sex influencing genic complexes and therefore homogametic. The male plant is assumed to be heterozygous for both of these two pairs of genic complexes but is digametic, as far as these two pairs of factors are concerned, because of extremely close linkage of the factors concerned.

As a final thought the author wishes to express the opinion that he considers that the solution offered need not necessarily be the final answer to the problem at hand. It is judicious to anticipate the suggestion that discoveries may be announced in the future which will render inadequate the simple analysis presented here. It fits the facts as they are known today, especially as they have been observed by the author, and is offered in that light only.

SUMMARY

This paper presents the results and conclusions derived from a study of the inheritance of floral morphology and function in grapes.

Floral morphology in the grape is definitely constant and rather sharply defined in that only one type of flower is normally found on any one individual.

All grape flowers are considered to be morphologically and potentially hermaphroditic in that all possess both pistils and stamens, tho one or the other of these organs may be more or less undeveloped.

Three types of hermaphroditic flowers are recognized on the basis of their behavior as follows: (a) Functionally hermaphroditic; (b) functionally pistillate (male sterile); and (c) functionally staminate (female sterile). Intersexual types do not occur.

The failure of one or the other of the sexual organs to develop is ascribed to the inhibiting effect of definite genetic factor complexes which behave as suppressor genes, producing male and female sterility. The use of the latter terms is suggested when reference is to be made to functionally pistillate and staminate types.

Suppression of the female organ, the pistil, is due to a dominant factor complex, *So*. Suppression of the male organs, the stamens, is governed by a recessive factor complex, *so*. These two pairs of genic complexes are borne on one pair of allelic chromosomes and are so closely linked that crossing-over rarely, if ever, occurs between them.

The functionally pistillate plant is homozygous for both pairs of recessive genic complexes and accordingly is homogametic—$\frac{so\ sp}{so\ sp}$.

The functionally staminate individual as it occurs in the wild is heterozygous for both pairs of genic complexes, $\frac{So\ Sp}{so\ \ sp}$, but due to the extremely close linkage of the two factors is essentially digametic.

Because of the close linkage of *So* and *Sp* and the dominance of *So*, functionally staminate individuals will appear only in the progeny of crosses involving a functionally staminate parent.

Two genotypically distinct kinds of functional hermaphrodites are recognized as follows:

1. The heterozygous hermaphrodite, $\frac{so\ Sp}{so\ sp}$. This type gives both functionally hermaphrodite and functionally pistillate progeny in the ratio of 3:1 when interbred or selfed. When backcrossed to the functionally pistillate form typical 1:1 backcross ratios are obtained. When crossed with pollen from functionally staminate forms ratios of 1 functional hermaphrodite :1 functionally pistillate :2 functionally staminate individuals are obtained. Examples of this genotype are Concord, Catawba, Delaware, Chasselas Golden, Sultanina, and the majority of other hermaphroditic American varieties of bunch grapes and of *Vitis vinifera* as well.

2. The homozygous functional hermaphrodite, $\frac{so\ Sp}{so\ Sp}$. This type is true-breeding for functional hermaphroditism when crossed on either functional hermaphrodites or functional pistillates. When crossed with pollen from functionally staminate individuals, both functionally staminate and functionally hermaphroditic individuals may be expected in a ratio of 1:1. Only a few individuals of this genotype were found, *viz.*, Muscat Hamburg, Seneca, Secretary, Kensington, Stout Seedless, Sultana, Gros Guillaume, and four unnamed Station seedlings, Nos. 8536, 8537, 8717, and 10115.

In the majority of crosses for which ratios of functionally hermaphroditic to functionally pistillate individuals could be calculated, a deficiency of functionally pistillate forms was observed. This fact, coupled with the reports of a preponderance of functionally staminate over functionally pistillate individuals in the wild state, has led to the suggestion that the latter floral type may be associated with differential viability factors.

With respect to the possible mode of origin of dioecism in the grape from an original functional hermaphroditism, an hypothesis is presented whereby the former condition is assumed to have arisen from the latter as the result of two mutations affecting the suppression of one or the other of the sex organs of the functionally hermaphroditic flower. A dominant mutation resulted in suppression of the female organs, while a recessive mutation resulted in the appearance eventually of a form with suppressed male organs. The dioecious form is considered to have replaced the hermaphroditic form at an early stage in plant development as judged by the worldwide distribution of dioecism in the grape and the apparent lack of functional hermaphroditism in the wild state.

The statement is made that the functionally hermaphroditic forms of today may be surviving remnants of the primitive functional hermaphrodites or may have reappeared thru spontaneous germinal mutations affecting one or the other of the suppressor genes.

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