New York Agricultural Experiment Station.

GENEVA, N. Y.

TYPES OF FLOWERS AND INTERSEXES IN GRAPES WITH REFERENCE TO FRUIT DEVELOPMENT

A. B. STOUT



BOARD OF CONTROL

GOVERNOR NATHAN L. MILLER, Albany. COMMISSIONER GEORGE E. HOGUE, Albany. IRVING ROUSE, Rochester. FRANK M. BRADLEY, Barker. CHARLES C. SACKETT, Canandaigua.

CHARLES R. MELLEN, Geneva. JOHN B. MULFORD, Lodi. C. FRED BOSHART, Lowville. PETER G. TEN EYCK, Albany.

OFFICERS OF THE BOARD

CHARLES R. MELLEN, President. WILLIAM O'HANLON, Secretary and Treasurer.

STATION STAFF WHITMAN H. JORDAN, Sc.D., LL.D., Director.

†Albert R. Mann, A.M.,
Agricultural Economist.
George W. Churchill, Agriculturist.
Reginald C. Collison, M.S.,

Chief in Research (Agronomy).

†T. Lyttleton Lyon, Ph.D.,

Chemist (Agronomy).

JAMES E. MENSCHING, M.S.,

James E. Mensching, M.S., Associate in Research (Agronomy). James D. Harlan, B.S.,

Assistant in Research (Agronomy).
WILLIAM P. WHEELER.

Chief in Research (Animal Industry).
ROBERT S. BREED, Ph.D.,

Chief in Research (Bacteriology).

HAROLD J. CONN. Ph.D.,

Chief in Research (Soil Bacteriology).
†WILLIAM A. STOCKING, JR., M.S.A.,

Bacteriologist.
George J. Hucker, M.A.,
Assistant in Research (Bacteriology).

Assistant in Research (Bacteriology). Fred C. Stewart, M.S.,

Chief in Research (Botany).
†Donald Reddick, Ph.D., Botanist.
Walter O. Gloyer, M.A.,

Associate in Research (Botany).
MANCEL T. MUNN, M.S.,

Associate Botanist. ELIZABETH F. HOPKINS, A.B.,

Assistant Bo'anist.

Lucius L. Van Slyke, Ph.D., Chief in Research (Chemistry).

RICHARD F. KEELER, M.S.,

Associate in Research (Chemistry).

RUDOLPH J. ANDERSON, Ph.D., Chief in Research (Biochemistry).

†LEONARD A. MAYNARD, Ph.D.,

Biochemist.
Walter L. Kulp, M.S.,
Assistant in Research (Biochemistry).

Assistant in Research (Biochemistry).
ARTHUR W. CLARK, B.S.,

Associate Chemist.

MORGAN P. SWEENEY, A.M., WILLIAM F. WALSH, B.S.,

Assistant Chemists.

MILLARD G. MOORE, B.S., NATHAN F. TRUE, A.B.,

Assistant Chemists.

GEORGE A. SMITH, Chief in Research (Dairying).

James D. Luckett, M.S.A.,

Editor and Librarian.
LAURA G. COLLISON, A.B.,

Assistant Editor and Librarian.

Percival J. Parrott, M.A., Chief in Research (Entomology).

†GLENN W. HERRICK, B.S.A., Entomologist.

Hugh Glasgow, Ph.D., *Fred Z. Hartzell, M.A., (Fredonia), Associates in Research (Entomology).

CLARENCE R. PHIPPS, B.S., GUY F. MACLEOD, B.S.,

Assistants in Research (Entomology).

ULYSSES P. HEDRICK, Sc.D., Chief in Research (Horticulture). †ROLLINS A. EMERSON, Sc.D.,

Geneticist.

†WILLIAM H. CHANDLER, Ph.D.,

Pomologist.

*FRED E. GLADWIN, B.S. (Fredonia), ORRIN M. TAYLOR,

GEORGE H. HOWE, B.S.A., RICHARD WELLINGTON, M.S.,

RICHARD WELLINGTON, M.S.,

Associates in Research (Horticulture).

Associates in Research (Hornculture). THEODORE E. GATY, B.S.,

THOMAS O. SPRAGUE, B.S., HAROLD B. TUKEY, M.S.,

Assistants in Research (Horticulture).

JAMES S. LAWSON, Phm.B.,

Museum Preparator.

Jessie A. Sperry, Director's Secretary.

FRANK E. NEWTON, WILLARD F. PATCHIN,

LENA G. CURTIS,

MAE M. MELVIN, MAUDE L. HOGAN,

K. LORAINE HORTON,

Clerks and Stenographers.

ELIZABETH JONES

Computer and Mailing Clerk.

Address all correspondence, not to individual members of the staff, but to the New York Agricultural Experiment Station, Geneva, N. Y.

The Bulletins published by the Station will be sent free to any farmer applying for them.

TECHNICAL BULLETIN No. 82

TYPES OF FLOWERS AND INTERSEXES IN GRAPES WITH REFERENCE TO FRUIT DEVELOPMENT*

A. B. STOUT †

INTRODUCTION

The types of flowers in grapes have long aroused interest among both the growers and the breeders of grapes who are concerned not only with the quality and the productiveness of seeded varieties, but with the development of the seedless or partially seedless varieties. Breeders of grapes are also finding it desirable, if not necessary, to determine as fully as possible how the development of the desirable distribution of the sexes in the flowers may be regulated, controlled, or influenced by breeding and by selection of parentage.

It is well recognized that the production of fruit in any variety and in any seedling plant depends, first of all, on the development of stamens and pistils and their power to function as sex organs in fertilization and in fruit and seed formation. This is well illustrated by the flower types of the best varieties of grapes now in general cultivation.

Self-fruitful varieties like the Delaware, Niagara, Winchell, and Concord have flowers in which both stamens and pistil are well developed and highly functional *inter se*. The stamens are *erect* or *upright* (Figs. 13–21) and their anthers contain pollen much of which is viable and capable of functioning in fertilization. Both kinds of sex organs are present and functional *inter se* in the same flower. The plants are *perfect hermaphrodites*. They set fruit to self-pollination.

Other varieties like Brighton, Lindley, Barry, and Massasoit have flowers whose stamens are recurved and more or less aborted and the pollen which they contain is much shrivelled and defective, and is entirely or almost entirely incapable of functioning in fertili-

3

^{*}Connected with Grape Culture Investigations.
†Members of the faculty of the New York State College of Agriculture affiliated with this Station.

^{*}This is the first report of work done in cooperation with the New York Botanical Garden.

[†] Director of the Laboratories, New York Botanical Garden.

zation (Figs. 32–39). Such varieties are slightly or even not at all fruitful if left to themselves for self-pollination. The pistils, however, are well formed and are capable of forming fruits containing seeds if properly cross-pollinated with good pollen. Since the stamens are more or less impotent these plants are called *imperfect herma-phrodites*. Such varieties have been called "self-sterile" and the pollen has been spoken of as "impotent" or "lacking in affinity" with pistils. There is, however, very general agreement among those who have investigated the condition of the pollen (Beach 1902, Booth 1902, Dorsey 1914, and Detjen 1917)¹ that the sterility is due to the poor condition of the pollen which is thus unable to function at all.

The so-called "self-sterility" in these varieties of grapes is, therefore, very different from the "self-sterility" of certain varieties of plums, apples, pears, and cherries, in which the flowers are perfect but the viable pollen is capable of functioning only in certain crossfertilizations with other varieties or other individuals. In the grape the sterility, it appears, is due solely to imperfect development of stamens and pollen. In the plum the pollen is physiologically incompatible with the female elements of the same plant, of plants of the same clonal variety, and also of certain other plants of diverse origin. In progenies grown from the seed of plants having this type of sterility (Stout 1918, 1920) all degrees of self- and cross-compatibilities and incompatibilities are often in evidence.

Studies made of grapes indicate that the imperfections in the stamens very generally, but not always, involve a recurving of filaments which gives a very different flower from that of the perfect hermaphrodite with its erect stamens.

Among all wild species of American grapes and in seedlings of cultivated sorts another type of flower, the purely staminate, has long been recognized. In this the pistil is much aborted and entirely functionless or is even lacking, but the stamens are well developed and yield much viable pollen. A plant with such flowers is highly fertile as a male parent in cross-pollination but is itself fruitless. It appears that wild species of American grapes consist only of staminate plants and imperfect hermaphrodites except perhaps for rather rare cases when individuals are found bearing some or even all perfect flowers.

Still another type of flower is seen in the grapes that produce seedless or nearly seedless fruits. Here the pistils are capable of developing into fruits but the ovules, if present, do not develop into seeds. According to Müller-Thurgau (1898), the fruits of the seedless raisins develop under the stimulus of pollen-tube growth. Pollination causes development of fruit but does not result in seed formation. Such varieties as Sultana and Sultanina, therefore, are fully seedless when grown under ample opportunity for both selfand cross-pollination. This seems clearly to indicate that in the fully seedless varieties no ovules capable of developing to full maturity are present. Nothing definite seems to be known regarding the exact origin of these seedless varieties and no seedless grape has yet become of commercial value in the eastern United States. The types of flowers which they possess have, however, been observed among seedlings and are to be considered in judging the value of the various flower types appearing in seedlings.

It seems certain that the flowers borne by the greater number of seedlings obtained in breeding grapes can be classed broadly as (1) staminate, (2) perfect hermaphrodite, and (3) imperfect hermaphrodite. No purely female types are known. For describing the general heredity of sex in grapes, such a grouping is useful (Hedrick and Anthony 1915, Detjen 1917). It has, however, been recognized that a sharp distinction between these types does not exist. As Booth (1902) remarks "the whole path is marked by transitional forms; thus there are no distinct classes of self-sterile and self-fertile grapes, but all gradations exist from one extreme to the other." It is in the study and selection of these intergrading intersexual forms that the possibility of finding types with the degree or kind of femaleness which exists in the seedless types seems most promising.

In continuing the studies of the inheritance of sex in grapes in progress at the New York Agricultural Experiment Station, and especially with reference to the production of the flower types that give seedless fruits, it has seemed advisable to describe in more detail the variations in the development of the flowers. A general survey has revealed at least one new type of flower here designated as having crinkled stamens, a wide range of variations in the length of stamens among flowers classed as perfect hermaphrodites, and various intermediates between the typically upright and the reflexed

¹See Literature Cited, p. 15.

types, and also that the seedless sorts are characterized by what we may call strong maleness and weak femaleness.

MATERIAL AND METHODS

The flowers described in this bulletin were all obtained in the Station vineyards at Geneva. Here are grown many named varieties of European and American grapes which afford material for a study of the flower types found in varieties whose performance in fruit production is well known. There are also several thousand seedlings blooming and fruiting that include first, second, and third generations of progenies from known parentage. These seedlings afford most excellent material for studies of variation in flowers and in fruit production, and in general of the inheritance of sex.

In making special examination of flowers, clusters in the height of bloom (parts of clusters were taken when the plant bloomed sparsely) were placed in paper bags and taken to the laboratory. The flowers were examined under low powers of the microscope and drawings made to a scale by careful measurement with a Stufen ocular micrometer. The germination of the pollen was tested with 5, 7.5, and 10 per cent cane sugar in 1 per cent agar. These media were run into test tubes with about 5 cc. per tube, and the tubes plugged with cotton and sterilized in an autoclave for 20 minutes at 15 pounds pressure. A fresh tube of each was used each day. These were placed in a water bath to keep the media liquid. Drops about 1 cm. in diameter were conveyed to glass slides by a glass rod and pollen grains were sown on them after they had cooled and solidified. The cultures were placed on clean glass racks over water in "museum jars" and kept from 18 to 24 hours in a constant temperature chamber at 68° F.

The fertility of the pistils and ovules in the flowers was judged by the production of fruit and seed under open field conditions. Complete data on these points are available in the records of the Department of Horticulture at this Station.

DESCRIPTION OF FLOWER TYPES

STAMINATE FLOWERS

Figures 1 to 5, illustrate typical staminate flowers of five seedlings. In Figs. 1 and 2 no pistil is in evidence or if present it is a mere lump

of tissue within and at the base of the cup formed by the nectaries. In Figs. 3, 4, and 5, rudimentary pistils are noticeably present, but in Fig. 3 there appears to be no stigmatic area. Engleman (1883 p. 9), Booth (1902), and Dorsey (1912) have pointed out that in most if not all staminate types there are present rudimentary pistils in various stages of abortion with or without stigmatic surfaces. No fruits of any kind are produced by these five plants.

The stamens of the single flowers and of all flowers of any given plant are remarkably uniform, but the length of filaments and size of anthers differs in different individuals. All those here illustrated (Figs. 1 to 5) would probably be classed as having upright stamens but in Fig. 2 the stamens are somewhat recurving. The pollen from all but Fig. 2 germinated excellently, with about 95 per cent of all grains forming tubes. The plants of this class are characteristically strongly male with femaleness not at all or only feebly expressed.

In wild species of American grapes, purely staminate plants are frequent, but such plants are rather infrequent among seedlings derived from cultivated varieties. From observations in the field, the writer is inclined to consider that staminate flowers of wild species tend to have rather long stamens, but a comparative study of many individuals of the different species is needed to determine this point.

SEEDLESS AND NEAR-SEEDLESS TYPES

The writer has not yet had opportunity to study the flowers of the seedless varieties of Vinifera grapes that have long been in cultivation in Southern Europe and more recently in California. Special attention has, however, been given to flowers of those seedlings at the Geneva Experiment Station that produce seedless or near-seedless fruits.

The flower shown in Fig. 6 is typical of four completely seedless plants that are seedlings of the "Concord Seedless." In 1913, Mr. E. H. Wetmore of Rushville, N. Y., sent a box of grapes (fruits) to the Experiment Station. They were borne on a vine that grew in a row of Concord and were mostly seedless. From the few seeds obtained from these fruits, four seedlings were grown and are now bearing good crops. The berries are "seedless" to the degree that the soft rudiments of seeds present are scarcely to be noticed when

8

one chews the pulp. The fruits produced in 1920 ranged from 7 to 18 thirty-seconds of an inch in diameter. They are of good size for seedless sorts, but smaller than the fruits of the Concord, and as shown in Plate III the bunches are well filled.

A typical flower from one of these plants is shown in Fig. 6. The stamens are unusually long, the anthers are well developed, and at least 95 per cent of the pollen germinated in each of two tests on the three strengths of sugar-agar media used.

These plants bearing seedless grapes are strongly male, but their seedlessness is, it seems to me, due to what we may properly call a weak grade of femaleness.

Figure 7 shows a flower of a plant bearing near-seedless or partially seedless fruits. The stamens are erect and well developed tho only of medium length. In tests for germination about 50 per cent of the pollen produced tubes. As is the case in Fig. 6, pistils of good size are present and from the appearance of the flower alone the plant would be considered as a perfect hermaphrodite. However, of the fruits examined, 27 were entirely seedless and ranged from 9 to 13 thirty-seconds of an inch in diameter; 8 fruits contained one soft seed each and ranged from 12 to 16 thirty-seconds of an inch in diameter; 52 fruits contained one well-developed seed each and were from 12 to 18 thirty-seconds of an inch in diameter; while only 5 fruits contained as many as two seeds each and these were 14, 15, 16, 17, and 18 thirty-seconds of an inch in diameter, respectively. The fruits are hence low in number of seeds, many are seedless, and none of the 1920 crop had more than two seeds. The fruits were of good quality and the bunches were uniformly well filled. (See Plate IV.)

This plant is a seedling from Triumph crossed with Delaware both of which are seeded grapes. A sister seedling bore fruits ranging from 15 to 19 thirty-seconds of an inch in diameter but none were seedless, altho no fruit contained more than two seeds.

A seedling derived from the cross Triumph x Dutchess has produced fruits ranging from 10 to 20 thirty-seconds of an inch in diameter. Many of the smaller fruits are seedless and of those examined none had more than two seeds.

All of these plants bearing seedless or near-seedless fruits have flowers with erect stamens with filaments of medium or long lengths and pistils of medium size. Descriptive records of the Station for

EXPLANATION OF PLATES

The flowers here illustrated are shown about four times their natural size. The original drawings for these were made to the same scale but there were some differences in the reduction for the various plates. Fig. 10 is enlarged about 110 times and Figs. 25, 37, and 39 about 350 times. The photos of Plates III and IV were taken natural size and are here reproduced as taken.



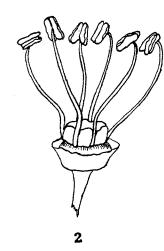


PLATE I

All figures are of staminate types of fruitless plants. Rudiments of pistils are present in Figs. 3, 4, and 5, but there is no stigmatic surface in Fig. 3. All are from seedlings: Fig. 1 of a plant of unknown parentage, Fig. 2 of America selfed, Fig. 3 of the cross Vitis Berlandieri x V. riparia, Fig. 4 of the cross Solonis x Riparia No. 616, and Fig. 5 of Croton selfed.



3

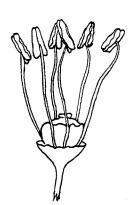


PLATE II

Fig. 6. Typical flower of plant producing seedless fruits, a seedling of Concord Seedless.

Fig. 7. Flower of near-seedless plant, a seedling of Triumph

x Delaware.

Figs. 8 and 9. Two flowers one with and one without pistil, borne in same cluster on a seedling of Solonis x Riparia. Fig. 10. Shows few potent and viable pollen among many shriveled grains from these flowers (x 110).

Figs. 11 and 12. Two flowers, both highly staminate one with rudimentary pistil, other with pistil functional in fruit and seed production. From a seedling of Dutchess x Seibel No. 2.

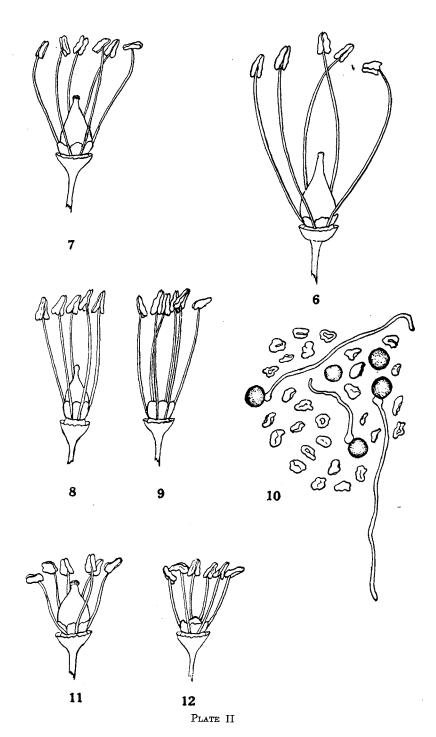




PLATE III.—CLUSTER OF SEEDLESS FRUITS BORNE BY SEEDLING OF THE CONCORD SEEDLESS. FLOWER OF THIS PLANT SHOWN IN FIG. 6

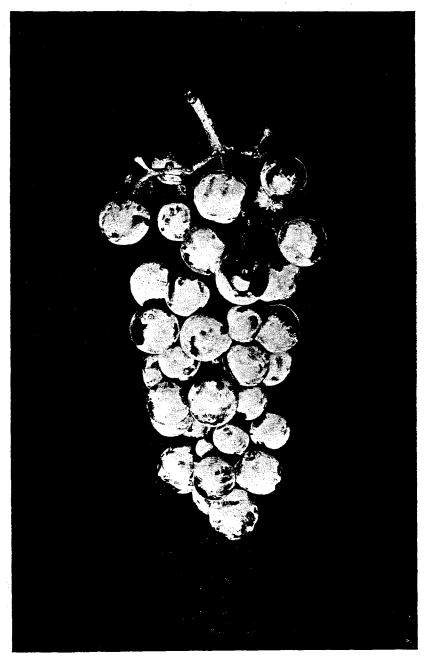


PLATE IV.—Cluster of Fruits, Many Seedless and none with more than two Seeds, borne by a Seedling of Triumph x Delaware. Flower shown in Fig. 7.

PLATE V

All perfect hermaphrodites with erect stamens. Highly functional both as males and females.

Fig. 13 of Wilder; Fig. 14 of Cottage; Fig. 15 of Worden; Fig. 16 of Concord; Fig. 17 of Seedling of Hexamer (selfed); Fig. 18 of Muscat Hamburg; Fig. 19 of Blauer Portugieser; Fig. 20 of Kensington; and Fig. 21 of seedling of Lindley x Niagara.

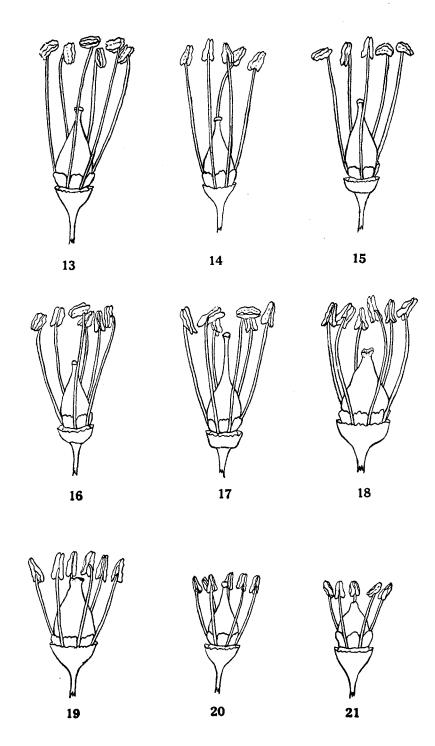


PLATE VI

Figs. 22 and 23 are flowers with crinkled stamens; Fig. 24 is a stamen 20 times natural size; and Fig. 25 the shrivelled pollen magnified about 350 times. For ancestry of the plants bearing these see page 11.

Fig. 26. Flower with crinkled stamens from a second generation

seedling of Salem x Worden.

Fig. 27. Flower with spreading stamens from seedling of Janes-ville selfed.

Fig. 28. Flower with strongly spreading stamens from seedling of Janesville selfed.

Fig. 29. Showing slightly recurving stamens of seedling of Clinton x Diana.

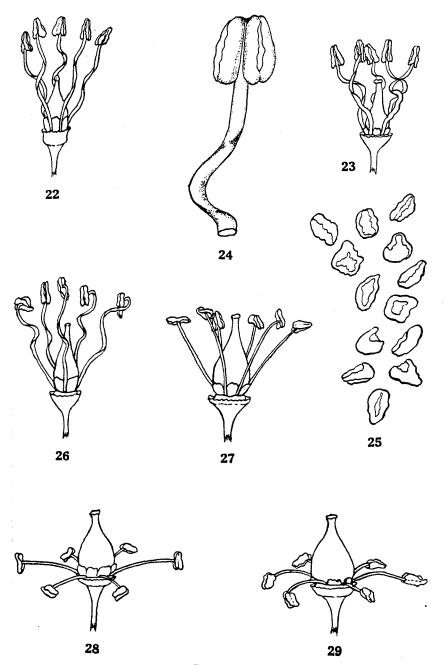


PLATE VI

PLATE VII

Fig. 30. Recurving or semi-reflexed stamens of seedling of Janesville selfed.

Fig. 31 flower just before, and Fig. 32 flower just after calyx is shed showing short stamens that become reflexed. (From Barry.)

Fig. 33. Flower of seedling of Noah selfed.

Fig. 34 flower of Aminia, Fig. 35 of Brighton, Fig. 36 of Massasoit, and Fig. 38 of Merrimac, all with strongly reflexed stamens. Fig. 37 pollen of Massasoit, and Fig. 39 of Merrimac enlarged 350

times.

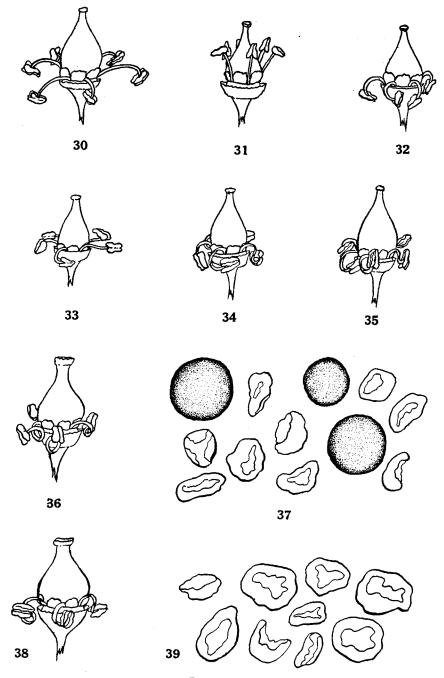


PLATE VII

flowers of such sorts as Hubbard Seedless and the Sultanina (the Thompson Seedless, a raisin grape widely cultivated on the Pacific Coast) indicate that these also have flowers of this general type. In respect to maleness the sex of these plants is highly developed, but their seedlessness shows that femaleness is weak and but partially developed. In the case of plants that produce seedless and seeded fruits in the same cluster there is indication that femaleness is irregular in its development and may appear in various grades among flowers of a single cluster altho such a mixing may not be apparent in the general appearance of the flowers, and not especially conspicuous in the general appearance of the clusters of fruit. (See Plate IV.)

Noll (1902) has called fruits which are produced without pollination parthenocarpic. The available evidence indicates that this is a relatively rare phenomenon. Such types should probably be classed quite differently than those in which pollination is required for any setting of fruit. They may perhaps be regarded as more strongly female or at least as strongly fruitful. There may be some question as to whether parthenocarpy is a phenomenon of vegetative or of reproductive vigor. However, the numerous grades of seedlessness which are found show, it seems to me, that when pollination is required seedlessness is to be regarded as a stage in the series of intersexes.

PLANTS WITH TWO OR MORE FLOWER TYPES INTERMIXED

In some plants it is plainly evident from an examination of the flowers that such extreme types as the purely staminate and what resembles the perfect hermaphrodite are intermingled in the same cluster. The latter may, however, give no fruit, seedless fruits, seeded fruits, or various mixtures of these. Figures 8 with 9 and 11 with 12, show this condition.

The plant bearing the flowers shown in Figs. 8 and 9 produced no fruit in 1920 which suggests that the pistils that are formed are functionless. The erect stamens are of good size and the anthers dehisce normally but only about 5 per cent of the pollen germinated. The grains that did not germinate were with few exceptions shriveled and aborted (Fig. 10).

The plant bearing the flowers shown in Figs. 11 and 12 produced a "light" crop in 1920, the clusters were decidedly "loose," the

berries irregular in size, and some of them were nearly seedless. Such crops are characteristic of many seedlings and also of some of the commercial varieties. A mingling of flowers in which there are various grades of development in the pistils is at least one of the causes of such incomplete fruiting. Purely staminate flowers and flowers with functionless pistils are fruitless, and other grades are seedless, near seedless, or strongly seeded. Irregular fruiting from year to year may, in some cases, be due in a large degree to variation in the proportions of the various types of flowers present.

PERFECT HERMAPHRODITES WITH UPRIGHT STAMENS

Marked differences in length of filaments, size of anthers, and size and shape of pistils are to be seen among flowers of this general class. The flowers illustrated in Figs. 13 to 20 are from well-known varieties. All of these sorts are highly productive of fruits that contain seeds. Altho the number of seeds characteristic of the variety may differ somewhat, all are strongly female and the fruitfulness depends on fertilization and on the development of seeds. As shown in the figures, the stamens of a variety may be so short that they scarcely reach above the stigma (Kensington, Fig. 20) and in another variety they may be at least twice that length (Cottage, Fig. 14). All grades between the extremes of length are to be seen among the varieties and the seedlings usually classed together as having upright stamens. In all the well-known cultivated varieties of this class, European as well as American, so far as tested by the writer, the pollen is remarkably viable with at least 75 per cent of all grains germinating in tests. In many seedlings, however, the pollen is mostly shrivelled and not viable in the germination tests, and the presence and general vigor of erect stamens is not a sure indication that the stamens are functional.

IMPERFECT HERMAPHRODITE WITH ERECT CRINKLED STAMENS

In these the stamens are ascending but the filaments are variously twisted or crinkled in irregular and incomplete spirals. (See Figs. 22 to 26.) The anthers appear, on general examination, to be perfectly formed and to dehisce normally (Fig. 24). Repeated tests for germination of the pollen were made for several plants bearing these flowers but no germination was obtained. So far as observed all pollen grains are irregularly shrivelled (Fig. 25).

The crinkled-stamen type of flower was found in each one of 34 sister plants, but the length of filaments and the degree of crinkling differed somewhat as is shown by comparing Figs. 22 and 23. In 1920 all but 2 of the 34 plants produced seeded fruit and of these 7 bore a "full" crop, 9 a "medium" crop, 9 a "light" crop, and 7 a "very light" crop. With the exception of two plants, these seedlings were able to function as females in fruit and seed production.

The ancestry of this series of 34 plants is well known for three generations. First, Winehell was crossed with Diamond (both classed as hermaphrodites with upright stamens), and Station Seedling No. 123 with upright stamens was obtained. This seedling was used as a pollen parent on Worden, also with upright stamens, and three seedlings, all with upright stamens, Nos. 931, 933, and 934, were obtained. The 34 plants derived from selfing seedling No. 933 were all of the type with crinkled stamens. Of the progeny obtained by selfing the sister plants, 931 and 934, 24 have bloomed and have only the normal erect stamens of the perfect hermaphrodite. As to length, the stamens of 1 were short, of 20 medium, and of 3 long.

It appears that the plants with this crinkled type of stamen are not able to function as males. Functionally their sex is quite like that of the imperfect hermaphrodites with reflexed stamens. One might consider that in these there is a combination of the "reflexed" character of filament with the "upright." The appearance of this type of flower in all of 34 sister plants after three generations of parentage with normal upright stamens suggests the phenomenon of the so-called mass mutation.

Another plant was found bearing flowers with crinkled but less erect stamens (Fig. 26). In this case the filaments may be considered as tending to be recurved. This plant is a seedling derived from selfing Station Seedling No. 4574 (having normal upright stamens), which was an offspring of Salem (reflexed) crossed with Worden (upright). In this case the reflexed character was present in one grandparent.

Whether the crinkled character of stamen is to be considered as due to a recombination of hereditary units, as an intermediate between reflexed and upright, or as a mutation, it is a new type of flower to be recognized in classifying the flowers of grapes.

FLOWER TYPES WITH SPREADING OR SEMI-REFLEXED STAMENS

Frequently among the seedlings there are plants with flowers whose stamens have nearly straight or slightly recurved filaments which at the time of complete anthesis stand at a decided angle from the axis of the pistil. In general these may be considered as intermediate between erect and recurved. Flowers of this sort from four plants are shown in Figs. 27 to 30. In these the anthers are well formed and dehisce quite normally, but the pollen was of irregular sizes, more or less shrivelled, and not viable in germination tests. These plants are able, therefore, to function only as females.

FLOWER TYPES WITH RECURVED STAMENS

The general character of this sort of flower is shown in Figs. 31 to 38, all but one of which are from well-known varieties long recognized as fully or very decidedly self-fruitless. The stamens may be strongly but simply recurved as seen in the flower of Barry (Fig. 32), extremely recurved and curled as in Massasoit (Fig. 36), or of various gradations between such conditions. The filaments are sometimes very slender. The anthers are in various grades of development; and in Barry (Figs. 31 and 32) thay are small in size, many appear to contain no pollen, and some do not dehisce. In other varieties the anthers are uniformly larger and dehisce well and a part of the pollen appears to be normal (Fig. 37).

The writer made extensive tests for germination of pollen both in varieties and in seedlings having reflexed stamens. In many cases all of the grains were irregularly shrivelled and devoid of granular contents. In other cases some of the grains became spherical on the sugar-agar media and appeared to have granular contents (Fig. 37), but in no case did any pollen from recurved stamens germinate. It should be noted, however, that seeds have evidently been obtained at the Geneva Station from selfing and crossing several of these varieties. Possibly a few of the grains are capable of germinating on pistils but incapable of germinating on media that give excellent germination of the pollen from staminate types and from hermaphrodites with normal upright stamens.

DISCUSSION AND CONCLUSION

A summary of the variations in the flowers of cultivated varieties of grapes and of seedlings from them shows that there are many grades in the relative development of pistils and stamens.

Complete loss of femaleness is seen in only a few cases, but various grades of rudimentary pistils are present that are incapable of yielding fruits of any kind. This evidence suggests that it is a weak grade of femaleness which is responsible for the development of seedless fruits. In near-seedless sorts, femaleness is of still another grade but below that of high seed production.

A complete morphological loss of stamens has not been found. The least male plants are perhaps among those with recurved stamens, small sterile anthers, and only aborted pollen. Such plants are able to function as females only. Plants with erect crinkled stamens and some plants with normal upright filaments are likewise unable to function as males because of impotent pollen. In the extremes there is complete loss of one or the other sex, at least functionally. Between these extremes there are various grades of relative development and functioning ability of pistils and stamens. In the perfect hermaphrodites both of these organs are highly developed and functional, and it is these types that include all of the most important and productive of the seeded grapes.

It appears that, in individual plants, the stamens are more uniform than the pistils; at least they appear to be rather uniform in respect to length of filaments and general character of anthers. The intermixing of flowers of several types in the same cluster seems to involve especially variations in the condition of the pistils. The most obvious of these are mixtures of staminate flowers and of perfect flowers that are capable of development into fruits with seeds. The type of pistil that produces seedless fruits may also be present.

Variations in the character of pistils in flowers from year to year have been observed. (See especially Detjen, 1917 for plant named "Hope.") There is some evidence that the fruit production of the self-fruitless varieties can be influenced by girdling and bending (Beach, 1902), but whether such treatment changes the character of the stamens by rendering them more potent as the results would perhaps suggest is not determined.

The variations in the morphological development of stamens and pistils and in their ability to function as sex organs are to be described as phenomena of intersexualism. The abortion of pollen in reflexed, in crinkled, and in other stamens is seen in flowers that are highly pistillate and functional as females. Conversely extreme loss of femaleness is seen in staminate types in which maleness is highly developed. In these extremes the loss of sex is one-sided. Such one-sided impotence is characteristic of intersexualism as distinct from the sterility of hybridity which tends to affect both sexes in the individual quite the same.

Cases of sterility in grapes due to hybridity are reported by Detjen (1919) in F₁ hybrids between Vitis vinifera (Malaga) and V. rotundifolia in which flowers of the external form of the perfect hermaphrodites are mostly or entirely sterile and impotent in both stamens and pistils. Such sterility appears to be largely absent in hybrids between V. vinifera and the more northern species of native American grapes. Many varieties known to have originated thus have perfect flowers with both sets of sex organs highly functional. A systematic study of known hybrids between V. vinifera and native species from which such a variety as Concord originated is needed to determine to what extent, if at all, sterility from hybridity is present along with intersexualism.

The results of the breeding work already obtained at the Station indicate clearly that the use of seedless and near-seedless plants as male parents in crosses with varieties that are strongly female (perfect and imperfect hermaphrodites) gives progeny that are strongly female and seed producing. The F₁ offspring of many crosses of standard seeded varieties with Hubbard Seedless have all been strongly pistillate, yielding seeded fruit. Weak femaleness (seen in seedless fruits) is in this case dominated or swamped by the strong femaleness of the seed parent. However, the seeded character of F₁ individuals is no index of the variation in intersexes that may appear in later generations in which the segregation of at least some plants bearing seedless fruits may be expected. The use of other seedless sorts in such crosses may, however, give different results.

The most effective course in breeding for the development of seedless sorts is suggested by the conditions of intersexualism. Most individuals and varieties producing seedless or near-seedless fruits are strongly staminate. The former can be used as male parents on the latter, which do produce a few viable seeds. Plants strongly male and seedless can be crossed with plants strongly male but weakly female and near-seedless and, also, the self-fertilized progeny of the latter may be obtained. In this way families weak in femaleness may undoubtedly be obtained in which a considerable number of individuals will produce seedless fruits.

LITERATURE CITED

Beach, S. A.

1902 Potency of the pollen of self-sterile grapes. N. Y. Agr. Exp. Sta. Bul. No. 223.

Booth, N. O.

1902 A study of grape pollen. N. Y. Agr. Exp. Sta. Bul. No. 224.

Detjen, L. R.

1917 Inheritance of sex in Vitis rotundifolia. N. Car. Agr. Exp. Sta. Tech. Bul. No. 12.

1919 Some F₁ Hybrids of *Vitis rotundifolia* with related species and genera. *N. Car. Agr. Exp. Sta. Tech. Bul. No. 18.*

Dorsey, M. J.

1912 Variation in the floral structures of Vitis. Bul. Torrey Bot. Club 39, 37-52.

1914 Pollen development in the grape with special reference to sterility. Minn. Agr. Exp. Sta. Bul. No. 144.

Engleman, G.

1883 Bushberg Catalogue. 3rd Edition.

Hedrick, U. P. and Anthony, R. D.

1915 Inheritance of certain characters of grapes. Jour. Agr. Research 4, 315–330.

Müller-Thurgau, Herman.

Abhängigkeit der Ausbildung der Traubenbeeren und einiger anderer Früchte von der Entwicklung der Samen. Landw. Jahrb. der Schweiz 1898. Abs. in Bot. Centr. 77, 135–138.

- Noll, F.
 - 1902 Fruchtbildung ohne vorausgegangene Bestäubung (Parthenocarpie) bei der Gurke. Sitzungsberich. der Niederrhein. gesellsch. f. Natur-u. Heilkunde zu Bonn 1902, 1-13.
- Stout, A. B.
 - 1918 Fertility in Cichorium Intybus: Self-compatibility and self-incompatibility among the offspring of self-fertile lines of descent. Jour. Genetics 7, 71-103.
 - 1920 Further experimental studies on self-incompatibility in hermaphrodite plants. Jour. Genetics 9, 85-129.