THE SECONDARY EFFECTS OF POLLINATION

Thesis for the Degree of M. S.

Welton Marks Munson

1892

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BY

WELTON HARKS MUNSON, B.S.

A THESIS FOR THE DEGREE OF MASTER OF SCIENCE.

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THESIS

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Introduction.

I. On the Immediate Influence of Pollen on the Mother Plant.

II. On the Developement of the Ovary, without Fecundation of the Ovules.

III. On the Amount of Pollen Required for Fertilization; and the Effects of Pollination on the Form and Size of the Fruit.

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THE SECONDARY EFFECTS OF POLLINATION.

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The change produced by contact of embryo sac and pollen tube is not confined to the mere vivification of one or more cells; though this is the chief end,- the primary object of all pollination. There are certain secondary effects which are of interest to the botanist and may be of great pracitical value to the horticulturist.

When there is a difference between male and female parents, the embryo partakes to a greater or less extent of the nature of both parents. In general, this influence is apparent first in the offspring of the cross; but in some instances there appears to be an immediate effect on the ovary or other portions of the female parent. In some cases also the pollen seems to have a direct stimulating influence on the ovarium, without effecting the impregnation of the ovules. Again, in certain instances the vigor of the plant seems suffi-

cient to develop a marked growth of the ovary in the entire absence of the male element. The form and size of the ovary are often materially affected by the application of different amounts of pollen to the stigma. In some plants more than one embryo is developed in a single ovule, indicating the possibility of superfœtation.

These, and other secondary problems arising in connection with the systematic amelioration of cultivated plants, are often of great practical importance.

The following notes can be regarded only as preliminary; as forming a basis from which to start in future work in this direction. Although some of the problems considered have been under discussion for more than a century, they are still unsolved. There has not been sufficient systematic study to warrant the formulation of general laws, and this study must necessarily extend over a long series of years. In the notes are embodied as concisely as may be, the more important results obtained by leading experimenters in this country and in Europe, together with some observations of the writer on the subjects in question. #

I. ON THE IMMEDIATE INFLUENCE OF POLLEN ON THE MOTHER PLANT.

Even before the sexual theory regarding plant reproduction was commonly accepted, the question of the immediate effect of pollen on the form and character of the female parent received the attention of careful observers. Bradley early gave directions for performing the operation of crossing and wrote: "By this knowledge we may alter the property and taste of any fruit by impregnating the one with the farina of another of the same class; as, for example, a Codlin with a Pearmain, which will occasion the codlin so impregnated to last a longer time than usual and be of a sharper taste; or if winter fruit be fecundated with dust of the summer kinds, they will decay before their usual time". ##

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I wish to acknowledge my special obligation to Prof. L.H.Bailey for certain notes and photographs, and for the free use of his private library.

Bradley, New Improvements in Planting and Gardening, 7th ed. (1739) p.18.

In 1745 Benjamin Cook, in a paper before the Royal Philosophical Society,# cited the appearance of russet apples on trees ordinarily producing smooth fruit, and the reverse, as examples of the effect of pollen. Other cases have been frequently noted as proofs of the existence of the same phenomenon. ## Even at this early date, however, careful experiments undertaken by Thomas Andrew Knight and others, tended to show that the apparent effects might be due to bud variation, or other causes aside from the action of pollen. Knight at this time wrote: ### " I have in some hundred instances introduced the pollen of one variety of the plum, the pear, the apple, the cherry, the peach, the melon, and other fruits into the blossoms of very different and opposite habits, and I have never, (although I have most closely attended to the results) found in any one instance the form, colour, size or flavour of the fruit belonging to such blossoms in any degree whatever changed or affected."

In 1865 Thomas Meehan opened discussion of the subject in the columns of the Gardener's Monthly, remarking: "For ourselves, without being satisfied that there is any material change in the quality of the fruit, we cannot deny there is some; and there may be much more than we at present imagine.---------- At any rate, we think it may be taken for granted that melons grown near squashes often have a suspicious squashy flavour, that gives some ground for the popular theory of mixing." $ The suggestion is further made that if this change be found to occur in squashes, the same law will apply to the whole region of fruits,——— an assumption which is altogether too broad. There is evidence which goes to show that within certain limits there is an immediate effect of the male element, but that those limits are quite restricted. As early as 1729 the presence of both white and blue peas in the same pod was observed, when two varieties of the different colors were planted near each other.$$ This fact has been repeatedly confirmed. In 1822 examples were presented to the London Horticultural Society. A variety known as Blue Prussian was crossed with a white variety. The resultant peas were yellowish white like the male parent.$$$ Laxton, in 1866, crossed the Tall Sugar Pea which bears thin green

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\# Philosophical Trans. 1745.
Trans. Lond. Hort. Soc. V.65.
Trans. Hort. Soc. V.67.
$ Gard.Month VII. 305.
$$ Philosophical Trans. XLIII, 525.
$$$ Trans. Hort. Soc. V. 234.

pods, with pollen of a purple podded variety. "The pod resulting was clouded with purple, while one of the peas was of a clear violet-purple tint and another was irregularly clouded with purple." The results, in so far as the changed color of the peas is concerned, were confirmed by Darwin. #

Crucknell ## cites an instance of apparent immediate influence in case of the pear. A single branch on a "Belle Lucrative" tree bore a few specimens resembling "Vicar of Winkfield." As Vicars were growing near, the conclusion is drawn that the fruits in question were affected by the foreign pollen. There is no reason to suppose, however, that this and the numerous cases of the appearance of russet apples on trees not usually russetted, are other than instances of bud variation, as pointed out by Knight. ###

Of about one hundred artificial pollinations performed by Charles W. Garfield of the Michigan Agricultural College, but three of the crosses showed any variation which could in any way be construed as the effect of pollen. " These were, First,- Wagener upon Tallman Sweet,— There was a modification of flavour quite noticeable, the first being sub-acid. Second, Tallman Sweet upon Astrachan. In this instance there was a manifest change in the color, flavor and shape. The apples were quite mild to the taste, the color was very much modified, and the form was that of a flat apple. Third, Tallman Sweet upon Wagener. The modification here was noticeable in all the specimens, in flavor and color."$

Professor L.H.Bailey in 1887, performed many crosses with different varieties of apples "and got no effect in any way, not even in season of maturity, or in texture." $$ Similar results were obtained by Crozier in 1888. More than one thousand crosses were made, and they were carefully observed during the season with a view to detecting any immediate effects. " The examination failed to show any differences which could be attributed to the influence of the cross, ------ In several instances different varieties were crossed upon the same tree, but the resulting fruit did not differ materially from each other,

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An. and Plts. under Domest. I. 428.
Gard. Month. IX, 165.
Trans. London Hort. Soc. V, 67.
$ Gard. Month. XVIII, 23 (Jan. 1876.)
$$ Proc. Am. Pom. Soc. 1887, 22.

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or from the remainder of the crop upon the tree." #

In many species, both wild and cultivated, sports, bearing fruit differing from the normal type are not uncommon. Dicecious plants of this character must necessarily receive pollen from an individual of a different character, but as a rule no effect is observed on the appearance of the fruit of either individual. A single plant of Mitchella repens, bearing white berries, was discovered by Mr.Meehan and removed to his grounds. Thus isolated, it produced no fruit, but in the natural state and fertilized by pollen from the red-berried form, the white fruit was produced in abundance. Prinos verticillatus as a rule has red berries, but a white berried form on the grounds of Professor Sargent regularly produced white fruit, though necessarily receiving pollen from the red form. ##

On the other hand, instances are cited to show that there is a marked effect on the color of flowers when two varities of different color are in close proximity. White verbenas, growing by the side of a pink variety are said to have produced striped flowers on the side of the plant next to the pink variety— the other side of the plant retaining the white color. ### Similar instances of changed color in case of phlox and petunias have come under my own observation, but in each of these cases the plants were so situated that the change could not be construed as due to the influence of pollen.

If pollen exerts a modifying influence on the character of the fruit, we should expect the color of black grapes to be less intense if fertilized by pollen from white varieties, than if self-fertilized, or crossed by other dark varieties. That such influence is doubtful, however, is indicated by the work of Goff, of Crozier and others.

In 1886, Goff crossed several varieties of black grapes with pollen from a white variety — the Lady Washington. Other flowers on the same vines were self fertilized. At maturity it was impossible to detect any difference either of color or of flavor between the self fertilized and the crossed berries of the same variety. $ Similar results were obtained by Crozier at the Iowa Experiment Station in 1888. $$

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\# Crozier, Bul 3. Iowa Ag. Exp. Sta., 92.
Gard. Month. XXVII, 116.
Berckmans, Am. Agriculturist, July 1889, 344.
$ 5th Rep. N.Y. Ag. Exp. Sta. 180.
$$ Ag. Sci. II 319.

The cotton plant furnishes an instance in which there is apparently unmistakable evidence of the immediate effect of foreign pollen. In 1890 at the Georgia Experiment Station flowers of upland cotton, Gossypium Barbadense (?) were crossed with pollen from common Okra, Hibiscus esculentus. Apparently perfect bolls of cotton were formed,but in every instance the seed failed to germinate when planted. The reciprocal cross resulted in apparently normal Okra seeds, but the offspring varied from the normal in time of flowering and fruiting. #
In 1891 the work was repeated, and Director R.J. Redding in a private letter to the writer reports, "bolls of cotton, the result of cotton blooms pollenized with okra pollen this year, in which one and sometimes two of the carpels contained a very small quantity of lint adhering to the seed while the other divisions of the ovary were abortive."

It was early observed ## that there is an immediate visible effect of foreign pollen on corn, extending in many cases even to the receptacle, and the repeated confirmations by Crozier, Sturtevant,### Kellerman, $ Tracy $$ and others would leave little doubt as to the accuracy of the observations.

That there is a difference in varieties, in the readiness with which the influence of pollen is shown, is altogether probable. Sturtevant lays down the general proposition: " Under the conditions of ordinary seed, maize does not in general show the effects of current cross-fertilization, the exception being the sweet corns which exhibit the influence of current foreign pollen very readily." The proposition is based on the study of about one hundred and twenty five named varieties, including flint, dent, pop, and sweet corns. That the flint and dent varieties often exhibit a change the current year, however, is abundantly proved by the work of the other experimenters referred to; though all agree that the change is most readily seen in sweet corn, and least so in the flint varieties. In this connection, also, Sturtevant makes the statement that:"cross-bred corn has a greater tendency to current cross-fertilization than has purely bred corn" $$$ —— a condition we should naturally

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\# Exp. Sta. Record, III. 2, 135.
Philosophical Trans. XLVII, 206.
3rd Rep. N.Y. Exp. Sta,. 148.
$ 2nd Rep. Kan. Exp. Sta.., 288-335, (1889)
$$ Rep. Mich. Hort. Soc. 1888, 43.
$$$ 3rd Rep. N.Y. Ag. Exp. Sta., 149.

expect from the variable tendency of hybrids and cross-breeds. While there would seem to be no doubt as to the immediate influence of foreign pollen in the case of corn, it is not improbable that what is in reality seminal effect, may sometimes be credited to the immediate action of foreign pollen.

Darwin # cites numerous instances to prove the existence of an immediate effect of crossing and though some of the examples to which he gave credence are now discredited, many of them are apparently well authenticated.

Seeds of Matthiola annua are normally of a light brown color, while those of M. incana are violet-black; yet M. annua crossed by M. incana yielded about fifty per cent of black seeds. Flowers of the orange fertilized by pollen from a lemon tree produced fruit bearing a longitudinal stripe of peel having the color, flavor and other characters of the lemon. Recent observations in this country and in Europe would appear to confirm the statements regarding citrus fruits.## Sabine ### cites an instance in which the form of the ovary of Amaryllis vittata was altered by the application of foreign pollen while Maximowicz made reciprocal crosses between Lilium bulbiferum and L. davuricum and found " each species produced fruit almost identical with the pollen bearing species." $ Fritz Müller crossed Cattleya Leopoldi by Epidendron cinnabarianum, and obtained a marked change in the form of the seeds.$$

Rhododendron dalhousiæ crossed by Rhododendron Nuttallii, is cited by Darwin as an example of the increased size of ovary resulting from the action of foreign pollen, while Arabis blepharophylla crossed by A. soyeri produced pods larger than either parent species. $$$

Darwin also gives credence $$$$ to the story of the St. Valery apple, the stamens of which are abortive, and being artificially pollinated, the fruits are said to differ from one another in size, flavor and color.— resembling in character the various kinds by which they have been fertilized.

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\# An. and Plts. under Domest. I. 428 et seq.
\## See Repts. Am. Pom. Soc. 1889 and 1891.
\### Trans. Lond. Hort. Soc. V, 69.
$ Darwin. An. and Plts. under Domest. I. 431.
$$ Ibid.
$$$ Darwin, An. and Plts. under Domest. I. 432.
$$$$ Ibid.

In the cultivation of pistillate varieties of strawberries, it is usually considered necessary to set some variety with well developed stamens in the immediate vicinity to furnish the pollen requisite to the fertilization of seeds, and consequent development of the receptacle. It is believed by many growers that the character of these pistillate varieties may be varied at will, by using different varieties for the male parent. In other words, it is believed that there is an immediate effect of the male element in determining the time of maturity, the color, the shape, and even the flavor of the receptacle of the variety crossed. If this theory be based on fact, it is of no small practical importance. If it were true, that in all cases, or that as a rule, the fruit partook of the character of the male parent, there could be no fixed character to any pistillate variety. But will the facts warrant the assumption that this immediate effect in the case of strawberries is by any means universal, if common?

Personally I have conducted no work bearing upon this point, but several experiments have been performed by careful observers, and the results obtained by them are of interest in this connection. The results as published differ considerably, but in general, the weight of authority goes to show that the receptacle is not materially affected by the male element.

At the meeting of the American Pomological Society, in 1885, extended and spirited discussions of this subject were held. Professor W.R. Lazenby, of the Ohio Experiment Station, had found the influence of the male element decidedly manifest. When blossoms of Crescent were fertilized by pollen from Downing, Vick, or Sharpless, the characteristic shape, texture and other qualities of the male used were impressed on the receptacle to such an extent that it was possible to determine the male parent from the general appearance of the crop. # A repetition of these experiments the following season, however, failed to give any marked results. ##

From an extensive field experiment conducted by Professor T.J. Burrill in 1884, it was found "easy enough to select individual berries conspicuously different from each other, as is always the case, but it was not possible to detect the slightest tendency towards a resemblance to the pollen bearer." ###

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Proc. Am. Pom. Soc. 1885, 66.
Rep. Ohio Exp. Sta. 1885, 107.
Proc. Am. Pom. Soc. 1885, 67.

In a similar experiment conducted the following year on the farm of P.M. Augur of Connecticut, like results were obtained. #

In none of the carefully conducted experiments of Goff and Hunn at the New York Experiment Station, have any immediate effects been discerned. Berries from Crescent blossoms, receiving the pollen of Lennig's White, were not different in color from those fertilized with Wilson or Sharpless pollen. Flowers fertilized on one side by pollen from the white variety, and on the other with Sharpless pollen were symmetrical in form and uniform in color. ##

Out of one hundred and sixty seven successful crosses made by Crozier, there was not an individual instance that pointed to a specific influence of the foreign pollen. ###

On the other hand, A.S. Fuller who has made a careful study of the subject since 1859, claims to have obtained very marked indications of an immediate directing influence on the form and size of the receptacle. $ Mr.Fuller attributes this apparent influence to the direct action of the pollen in stimulating the growth of the ovary or receptacle, without reference to the fertilization of the ovules. Admitting the stimulating effect, however, — and of this there seems to be little doubt — does the directing effect necessarily follow? The question is still an open one, but the results obtained from our work with cucurbits, with tomatoes and with egg plants, as well as the published results obtained by other observers, would point to a negative answer.

The nature of cucurbitaceous plants is admirably adapted to show the immediate effects of crossing if such occur. In a mixed plantation many of the flowers on any individual plant, when left to natural processes would necessarily receive pollen from very different sources. If now, there were an immediate effect of pollen, we should expect to find fruits of very different character on any given vine. Such is not the case, however. I have repeatedly looked for this difference but have never seen it; nor have I observed it when several flowers on the same plant were artificially crossed.with pollen from different varieties or species. Crozier and Bailey have repeatedly obtained like results. Bailey, whose crosses

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\# Proc. Am. Pom. Soc. 1885, 70.

\## 4th Rep. N.Y. Agr'l. Exp. Sta. (1885) 227; 5th Rep. (1886) 179; also Bul 24 (N.S.) 330 (1890).

\### Ag. Sci. IV. 287.

$ Proc. Am. Pom. Soc. 1885. 68.

of cucurbits run up into the thousands, asserts positively that "there is no immediate influence whatever, except such as is due to imperfect development caused by insufficient or impotent pollen." #

In our own work with tomatoes and egg plants there has in no case occurred an instance of immediate effect other than alteration of form due to insufficient pollen. During the past winter numerous crosses and hybridizations of tomatoes have been made. The accompanying photographs of the most violent of these crosses indicate the entire absence of apparent effect.

Figures 1 and 2 represent the "Lorillard", crossed by pollen of the "Currant", —— (Lycopersicum esculentum X L. Pimpinellifolium). The Lorillard is a smooth, nearly spherical variety of medium size, and as grown under glass seldom weighs more than three or four ounces.

Figure 1.

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Bul. 25 Cornell Univ. Exp. Sta., 181. (Dec. 1890).

Figure 2.

As will be seen, the fruit is in every respect typical of the Lorillard. The offspring from this cross, however, show unmistakable evidences of the influence of the male parent, both in the habit of the plant and in the character of the foliage and flowers.

Figures 3 and 4 are photographs of a cluster in which each fruit has a different male parent. As in the other case there is no apparent effect on the form of the fruit; and the seeds gave no indication of different parentage, —— all were apparently typical Lorillard seeds.

In the offspring, the differences are very marked. The lines are sharply drawn between the crosses with Peach and Currant, while the Lorillard is apparently unaffected by either of the others, —— indicating that there was no error in the operation, also that there has been no transfer of influence along the short interval between the peduncles.

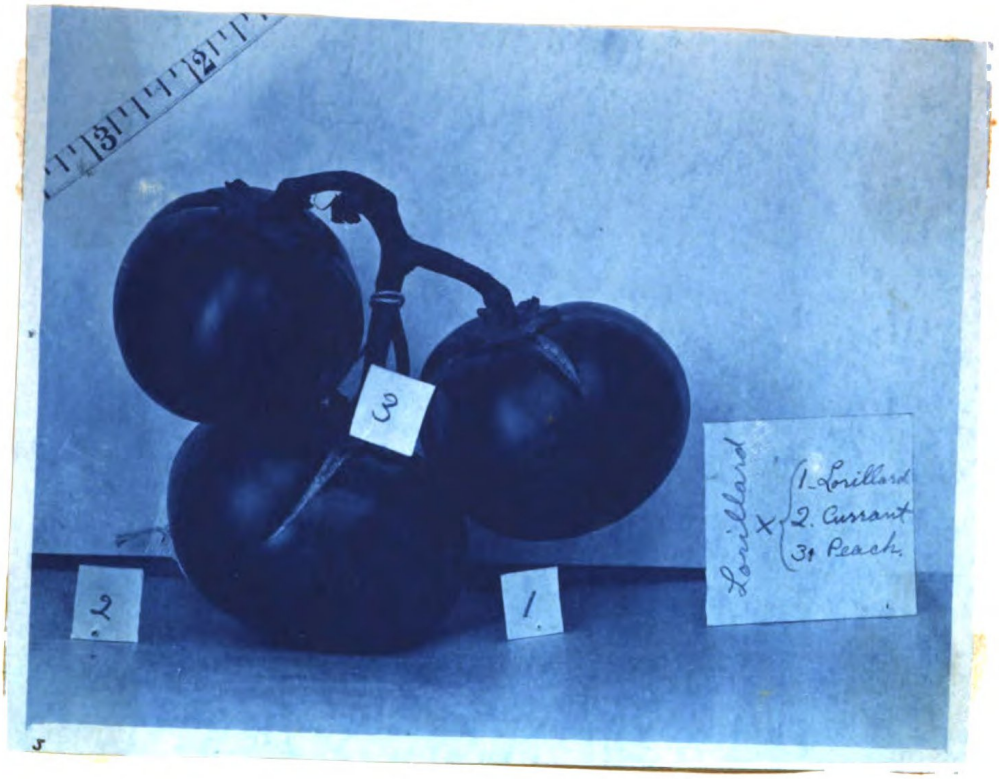
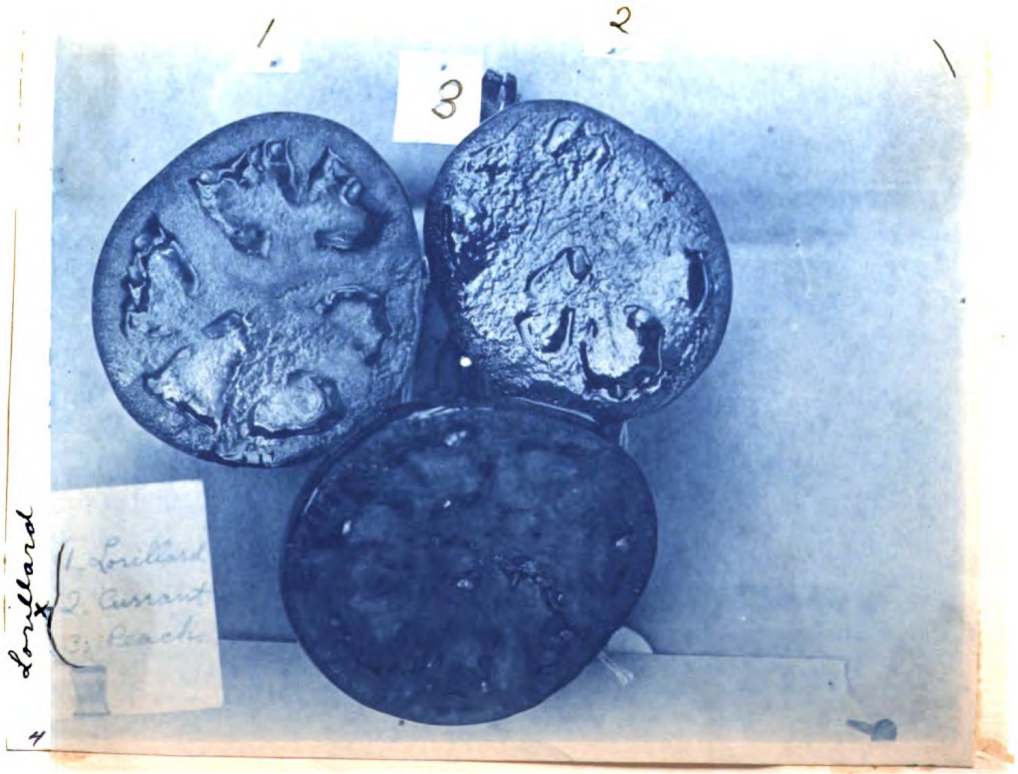

3
2
1
Lorillard
x
1. Lorillard
2. Currant
3. Peach

Figure 3.


1
2
3
Lorillard
x
1. Lorillard
2. Currant
3. Peach

[illegible]

In an extended series of experiments with egg plants, conducted for three consecutive years at the Cornell University and the Maine State College, the most widely varying types have been crossed. In no instance, however, has there appeared an immediate effect of the male parent. The little Round White, when crossed with pollen from Black Pekin, differed in no respect from other fruits on the same plant. But the offspring of this cross showed very marked variations. The same facts were observed regarding several other crosses.#

As before noted, instances have been reported, in which the color of flowers was apparently changed by the action of foreign pollen the current season. An instance of such change has never come under my observation, though I have made numerous crosses of different varieties of Tropaeolum, Fuchsia, Silene, Phlox, Petunia, and other ornamental plants.

As indicating the range over which the study of the subject has extended, a partial list of the species considered by different observers is given:

—— Species in which immediate influence of pollen is said to have been observed:

Amaryllis vittata
Arabis blepharophylla.
Cattleya Leopoldii
Citrus Aurantium
Gossypium Barbadense. (sp. ?). ##
Lilium bulbiferum
Lilium davuricum
Matthiola incana
Phaseolus vulgaris
Pisum sativum
Rhododendron dalhousiæ
Verbena sp.
Zea mays.

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\# Bailey & Munson, Experiences with Egg Plants, Bul. 26. Cornell Exp. Sta., p. 14.

The common "Upland" or "Short Staple" cotton and the "Sea Island" cotton are usually classed as varieties of G. Barbadense, but some authorities regard them as distinct species.

Species in which no immediate effect appears to occur:

Cucumis melo.
Cucumis sativus.
Cucurbita maxima.
Cucurbita moschata.
Cucurbita pepo.
Datura Stramonium.
Datura inermis.
Fragaria virginiana.
Lycopersicum esculentum.
Lycopersicum pimpinellifolium.
Mitchella repens.
Prunus Americana.
Prinos verticellatus.
Pyrus malus.
Pyrus Torringo.
Pyrus Soulardi.
Vitis labrusca.
Petunia violacea.
Phlox Drummondii.
Silene armeria.
Tropæolum minus.
Fuchsia sp.-

The above lists are probably incomplete, and must necessarily be regarded as tentative. As yet there are no satisfactory data on which to base general conclusions. It would be unwise at the present time to assert that the directing influence of pollen does or does not as a rule extend beyond the fertilization of the seed. It seems not improbable that pollen from a vigorous plant, may make an imprint of its character on the female organism which shall be different from that of a less vigorous male parent. It is probable, however, that the vigor and inherent vitality of the plant operated upon usually determines whether this be manifested. Some species show apparently unmistakable evidence of the influence of foreign pollen, - this is notably the case with peas and Indian corn.

On the other hand, cucurbitaceous and solanaceous plants seem to resist all foreign influence; while rosaceous plants are in dispute, with the weight of authority tending to show the absence of immediate influence.

II. ON THE DEVELOPMENT OF THE OVARY WITHOUT FECUNDATION OF THE OVULES.

A common, though not universal law of reproduction by seed requires fertilization of the ovules as a condition necessary to the development of fruit. It is a matter of common observation that, as a rule, when pollination fails to result in fertilization, or when pollen is withheld, not only the pistil withers, but the entire flower decays and falls. (Pollination is used in the sense of cöition in the animal kingdom and does not necessarily result in impregnation). Instances are not infrequent, however, which point to a responsive action on the part of the pistil or other portions of the flower receiving pollen, while from an insufficient quantity of pollen, lack of affinity on the part of the species crossed, or some other cause which remains to be determined, fertilization does not occur. Examples of this are specially common in all of our cultivated fruits and vegetables.

About the close of the seventeenth century, (1691), Camerarius had observed # that a female mulberry tree once bore fruit though no male tree was in its vicinity. The berries, however, contained only abortive seeds. Plants of Mercurialis annua being then brought under observation, it was noticed that while the fruits were abundant and well filled out, they began to wither when about half ripe and not one produced perfect seed.

The instance of the mulberry is confirmed by Claypole who cites ## a case within his own observation in which a pistillate tree bears fruit abundantly every year though no staminate tree is in the vicinity, and no staminate flowers have been found on the tree itself. The "seeds" in these fruits, as in the other instances, contain no embryos. Whether this is a case of development in the entire absence of pollen, as circumstances would indicate, or whether there may have been a limited supply of pollen at hand, it is evident that the ovaries developed independently of any action on the ovules.

Dr. Masters is authority for the statement that certain varieties of pears habitually produce seedless and coreless fruit. ### In the same way it is not uncommon to find the capsule of many herbaceous plants fully developed while the seeds

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R.J. Camerarii Opuscula Botanici Argumenti, cited by Sachs — Hist. of Bot. 386.

Rep. U.S. Dept. of Ag. 1887, 318.

Nature, XXXV, 12. (Nov. 4, 1886).

are absent. M.Jean Sisley, a well known French horticulturist, found this to occur with great frequency in case of the geraniums and pelargoniums. Of one hundred flowers of Geranium platypetalum artificially pollinated, not one produced perfect seeds, and of a large number of capsules sent by another party, nearly all were without seeds. #

Naudin as a result of his studies of the genus cucurbita suggested the possibility of a specific effect of pollen in exciting growth of the ovary, and this theory is supported by Focke who says: "Pollen has two actions on the female organs, one on the seeds, and one in exciting the growth of the fruit." ## The theory seems plausible, and in view of the many examples of well developed but empty seed pods, it would seem that the stimulating action is alone exerted in some instances. These examples are specially common among peas and beans.

The accompanying photograph, Figure 5, represents the natural size of a Lima bean which failed to develop seeds, — the undeveloped ovules may be seen at the right.

According to Hildebrand in the case of several orchids, the plant's own pollen is necessary for the development of the ovarium; and this development takes place long before the pollen tubes have reached the ovules. ### So in these cases the pollen acts directly on the ovarium.

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Gard. Chron. N.S. IV, 654.
Focke, Die Pflanzen-Mischlinge. 447.
Botanische, Zeitung, No. 44 et. seq. Oct. 30, 1863 and Aug. 4, 1865, cited by Darwin, An. and Plts. under Domest. I, 434.

Figure 5.

Disregard of the fact discovered by Camerarius, but not emphasized by him, that certain diœcious plants occasionally have monœcious individuals, has led to many erroneous statements regarding the influence of the male element on the ovary. Hemp and Spinach have been cited # as examples of development without fertilization. It is well known, however, that both of these species have monœcious individuals, thus furnishing a source of error in observation.

The muskmelon, Cucumis melo, is another instance in point. This fact first attracted my attention when attempting to perform some artificial hybridizations between Cucumis melo and Cucumis sativus. The female blossoms on the variety under consideration ("Emerald Gem") were found to bear partially developed stamens. These stamens varied in size

Le Maout & Decaisne, -- System of Botany, 152.

and in the amount of pollen produced, but subsequent developments indicated that enough pollen may be produced to secure self-fertilization. —— In these cases of probable self-fertilization, however, there were no perfect seeds.

Darwin cites, on the authority of Dr.Hooker, an instance of the development of the ovarium of a certain orchid — Bonatea speciosa — as a result of simple mechanical irritation of the stigma. # That under certain conditions the ovary of some species may develop to a considerable degree entirely without the intervention of the male element seems to be beyond question. What the conditions are which insure this phenomenon is as yet uncertain. Exceedingly vigorous growth of the plant is certainly a first requisite, but there also seems to be an individual variation in this direction, with some species.

The fact that in growing English forcing cucumbers for market, gardeners never practice artificial pollination, as is necessary with the varieties commonly grown in this country, raised the question as to whether any pollen is required, and what proportion of the fruits would develop without fertilization.

Several different varieties have been under consideration at different times. In case of the "Telegraph", a long slender variety, more than twenty blossoms were covered with paper bags before expanding — thus preventing all possibility of the access of pollen. Out of this number, but two developed fruits. These were typical in form and of average size, — being about sixteen inches long and two and one half inches in diameter. They contained a large number of partially developed ovules —— some of them 3/8 inch in length —— extending nearly the whole length of the fruit. There were no perfect seeds, however, as shown by Figure 6.

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An. and Plts. under Domest. I. 434.

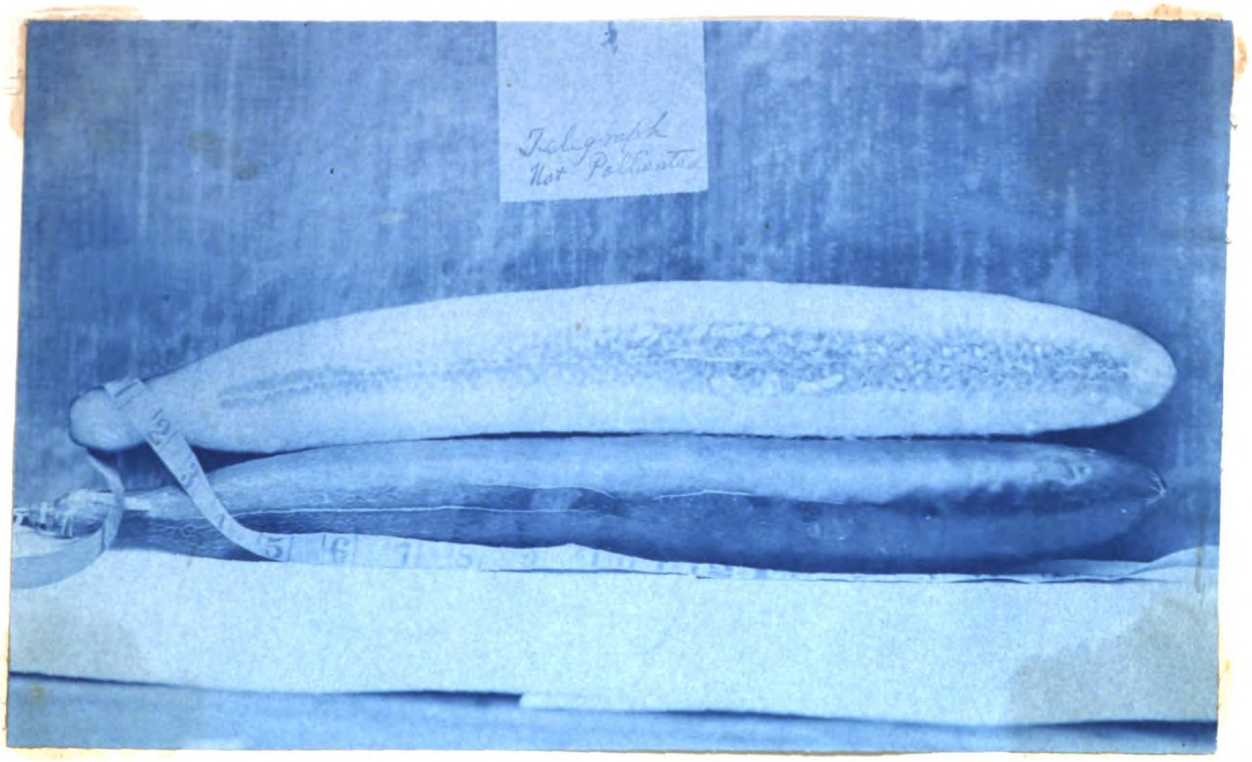

Figure 6.

Of ten blossoms of the variety known as "Sion House", covered as above, one developed fruit. Later many other blossoms were covered and some fruits were developed, but the percentage was about the same as before. The fruits, as with the "Telegraph", were straight and smooth and contained an abundance of partially developed ovules along the whole length of the fruit; but there were no perfect seeds.

Other fruits of both varieties, left to natural conditions, were examined and as a rule were found to contain no perfect seeds. Indeed, this absence of seeds is a matter of common observation, and is urged as a point of excellence in favor of the English varieties. In one instance two or three apparently good seeds were found, but no embryo was present, while most of the ovules were only one eighth to one fourth inch in length. There are few, if any, insects in a forcing house in mid-winter, which would be likely to carry pollen; and it is probable that fruits left to natural conditions received no pollen.

Other varieties exhibit characteristics peculiar

to themselves, when pollen is withheld. "Blue Gown", for example is almost invariably withered and shrunken at the apex or "blossom end", as shown in Figure 7. The same tendency is shown by the " Duke of Edinburg". No seeds are developed in these fruits, and at maturity they are often hollow at the lower end, as shown in Figure 8.

In several instances I have observed the development of fruits on the "Duke of Edinburg", when the blossom never expanded. One of these is shown in Figure 9.

Figure 7.

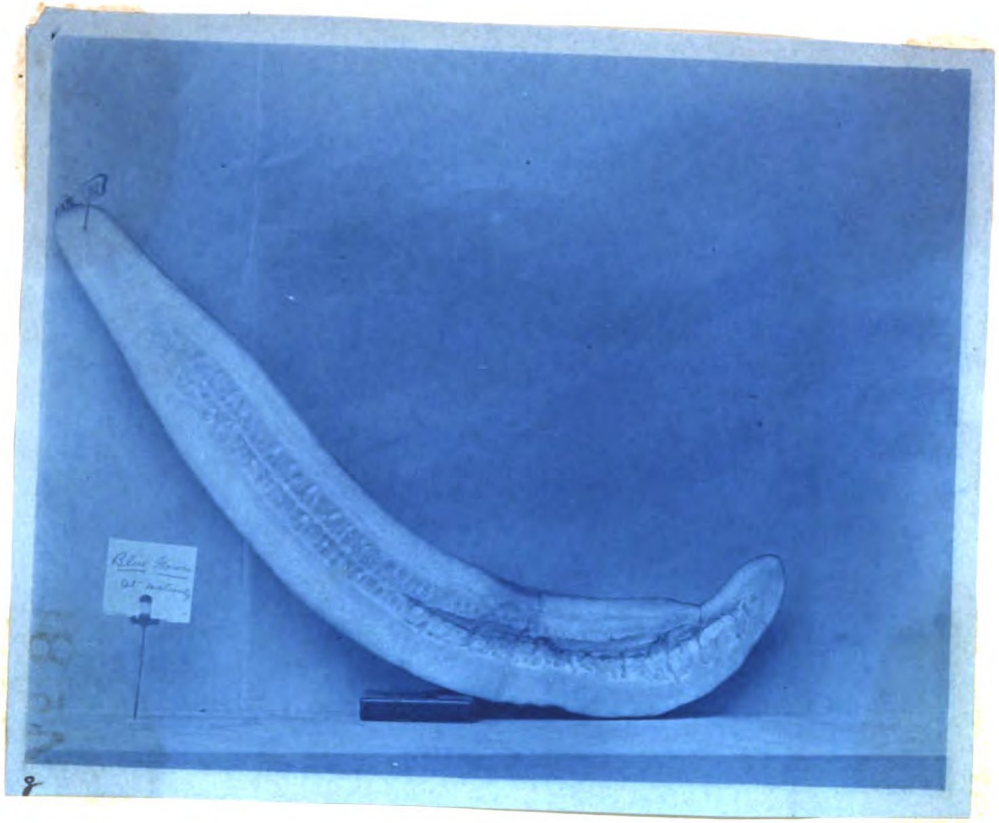

Figure 8.

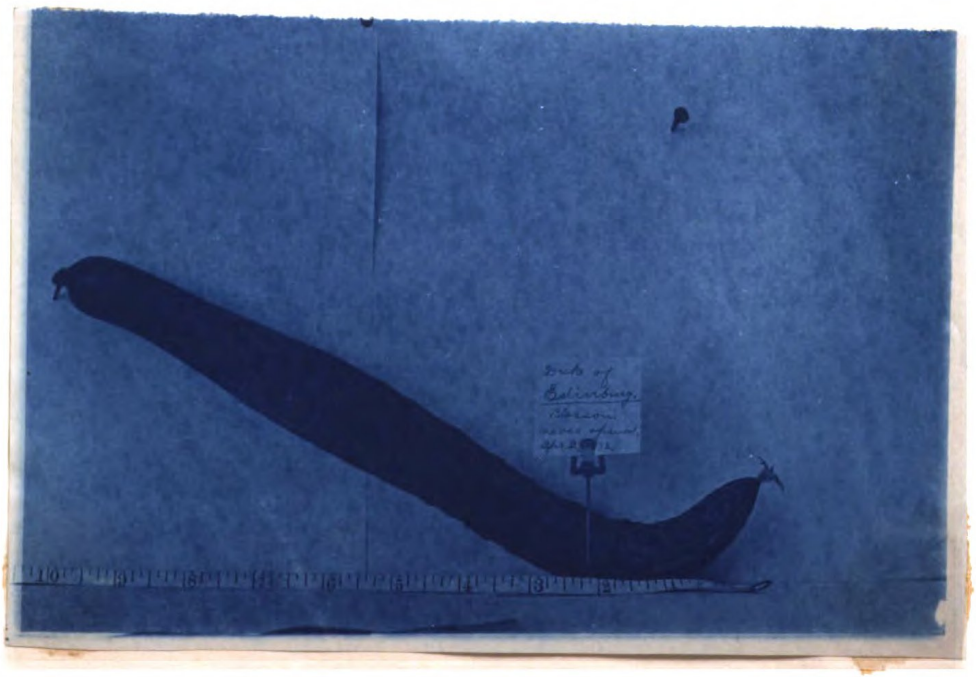

Figure 9.

In our studies of the egg plant — Solanum melongena, etc. — we have at different times secured well developed fruits from blossoms which had been castrated and covered with paper bags to prevent access of foreign pollen. In no case have perfect seeds been found. The first instance noted was in the summer of 1890, and the fact was published the following spring. # During the past winter, 1891-2, experiments in this line have been repeated on plants growing in the house. Out of fifteen blossoms emasculated and covered, two apparently good fruits developed. One of these when about six weeks old began to decay, and was picked, and photographed — see Figure 10. The other, at the present writing is still growing.

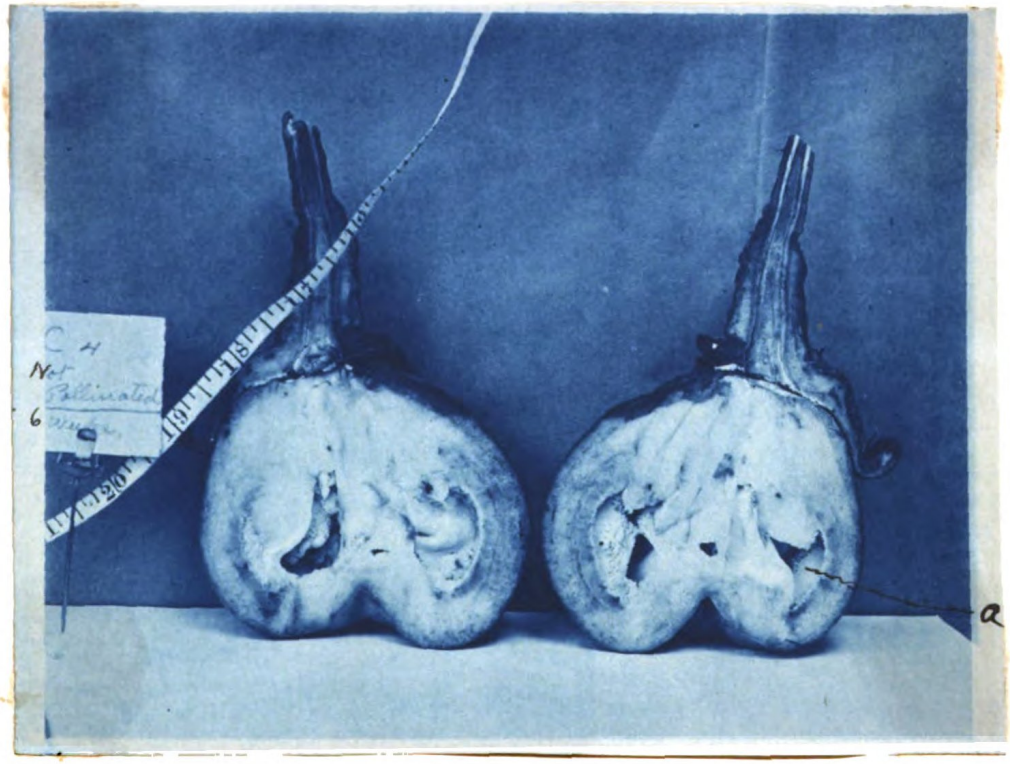

Figure 10.

As will be observed, the outer portions of the fruit grew much more rapidly than the inner, — the placentæ evidently requiring the stimulus of the growing ovules to induce

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Bailey & Munson, Experiences with Egg Plants, Bul. 26, Cornell Exp. Sta. 19.

development. The abortive ovules are seen at a, as minute brown particles. A very few of them — ten in the whole fruit — were partially developed,- indicating the possibility of a few grains of pollen having reached the stigma. The work was very carefully performed, however, and I am confident there is no error.

It is interesting in this connection to note the fact that these fruits have usually developed on cross-bred plants, rather than on fixed varieties,— a fact apparently in accord with the supposition before expressed, that excessive vigor of the plant is a prime requisite for the appearance of the phenomenon.

A further indication that excessive vigor of growth may affect the fruit, is in the abnormal development of the calyx of the egg plant in many instances, while the growth of the ovary is arrested. Usually the most prominent indication that impregnation has taken place, in the egg plant, is the rapid growth of the calyx. Many times, however, the calyx becomes much enlarged while for some reason the ovary fails to develop. I have frequently seen examples of this, in which the calyx was fully six inches long.

Another instance of the partial development of the ovary was observed in a Summer Crookneck Squash to which pollen of another variety was applied. The fruit attained about eight inches in length, and remained in this condition during the season. No perfect seeds were developed.

From the evidence adduced the fact seems well established that the ovary may develop and reach normal size without the corresponding impregnation of the ovules, and even in the entire absence of the male element. What the conditions are which induce this apparently abnormal condition, is not fully determined. It is evident, however, that vigorous growth of the parent plant is of first importance.

III. ON THE AMOUNT OF POLLEN REQUIRED FOR FERTILIZATION; AND THE EFFECTS OF POLLINATION ON THE FORM AND SIZE OF THE FRUIT.

Kœlreuter,# in 1761-66, found that with Hibiscus venetianus, fifty to sixty pollen grains were sufficient to produce more than thirty fertile seeds in the ovary. In Mirabilis jalapa, and M. longiflora, which have a one ovuled ovary, two or three, and in some cases even one grain was sufficient for fertilization. Now, according to Kœlreuter, the Hibiscus produced 4863 poller grains in a single flower, — or 81 times more than needed for actual fertilization. So also the Mirabilis produced about 300 grains, or from 100 to 200 times too much. It appears therefore that there is no relation between the amount of pollen produced by a plant, and the amount required for fecundation.

Since the time of Kœlrenter, little has been done toward determining the actual number of grains required for the fertilization of any given species; but the fact has been plainly demonstrated that the amount of pollen applied may have great practical importance in determining the form and size of the fruit, as well as the quantity of fruit produced.

In crossing strawberries at the New York Agricultural Experiment Station, ## the fact was plainly brought out that the proportion of berries secured depends upon the abundance of the pollen furnished by the variety used as a fertilizer, — a point which is of great moment if the same law holds under natural conditions. That there may be some doubt of this, however, is indicated by the fact that certain so-called pistillate varieties — notably the Crescent — at times mature fruit and apparently perfect seeds in the absence of any perfect flowering variety.

One grower of my acquaintance uses no perfect flowering variety, and succeeds admirably. I have never seen these plants, but it is well known that the pistillate varieties frequently produce plants having partially developed stamens, and it is probable that by unconscious selection, plants of this character have been increased to a considerable extent. In any case, the amount of pollen is necessarily quite limited.

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Cited by Sachs, Hist. of Bot. 408.

5th An. Rep. N.Y. Ag.Exp. Sta. 179.

That the amount of pollen used may have an important bearing in determining the form and size of the fruit is certain. This fact, which is of special importance to the horticulturist, is shown by our work with tomatoes.

In the winter of 1890-91, while crossing tomatoes, two stigmas in the same cluster of flowers, were given different amounts of pollen. The first was given a very small amount — ten to twenty grains — on one side of the stigma; the other was given an excess of pollen, the stigma being well smeared. The effect on the form and size of the fruit was very marked. The fruit receiving the large amount of pollen was of normal size and nearly symmetrical in form; while the other was small and deformed. The larger fruit developed an abundance of seeds and all of the cells were well developed; the smaller developed seeds on one side only, while the other side was nearly solid.

During the past winter the experiments have been repeated many times and the results have been uniformly similar to those detailed.

In the first case,— see Figures 11 and 12 — the flowers nearest the base of the cluster received an excess of pollen, while the other received a very small quantity on one side of the stigma. In another instance,— see Figures 13 and 14 — the flower at the base received the small amount of pollen, while the other was given an excess. Similar results were obtained, indicating that the relative position of the flower has no influence in determining this point. As will be seen from Figure 14, the seeds in this instance — but ten in number — were all born in one cell, and the deformity of the fruit was correspondingly greater than in other cases. The difference in size of the fruits was even greater in some instances than in those already cited, as seen in Figure 15.

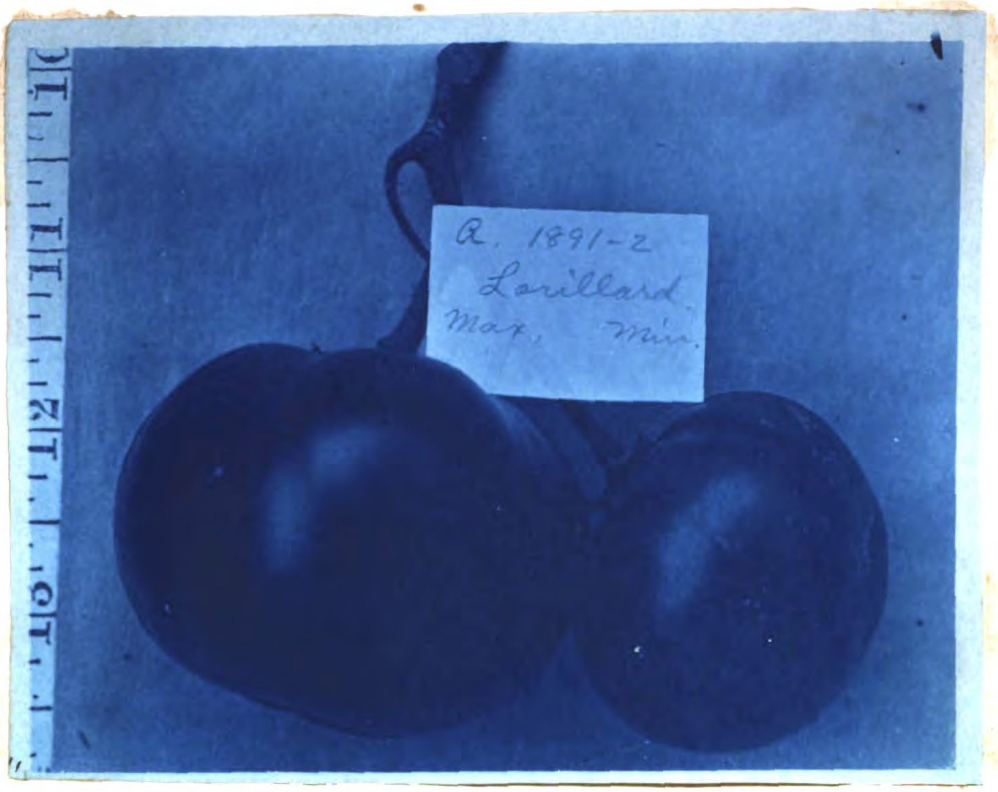

Figure 11.

Figure 12

Figure 13.

Figure 14.

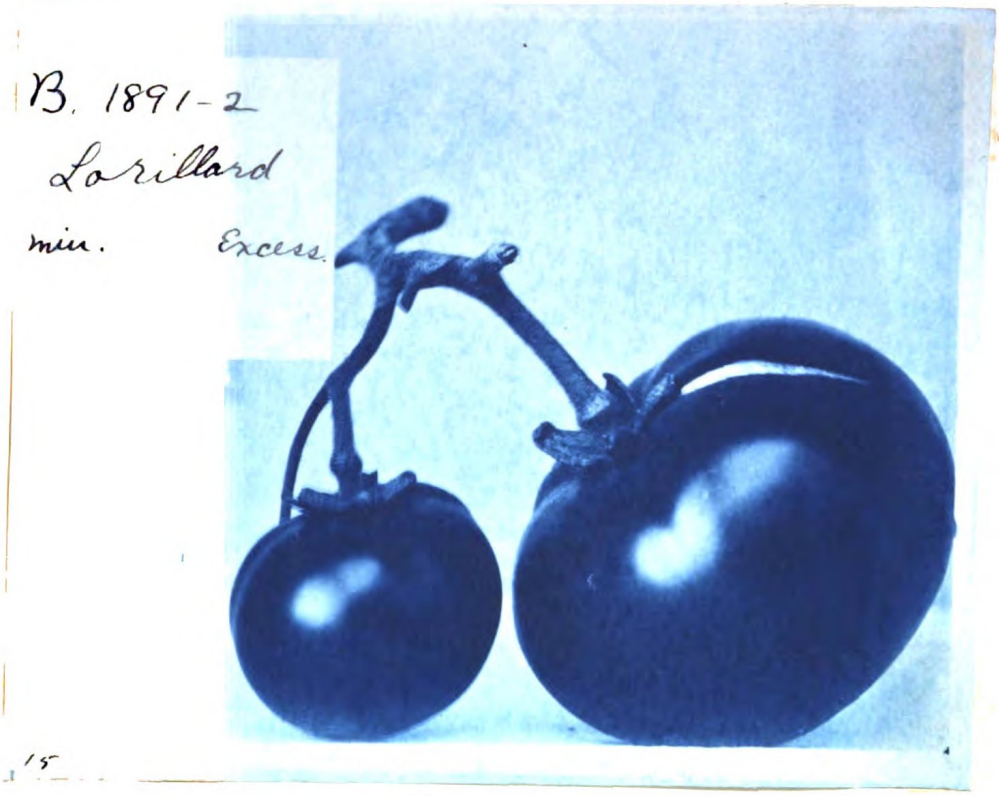

Figure 15.

The exact number of pollen grains necessary to insure partial development of the ovary, in case of the tomato, I am unable to state at the present time. Certain it is, however that the secondary actions of the pollen in stimulating the growth of the fruit is of no small importance. No doubt the greater development of the one side is largely due to fertilization of the ovules and the consequent growth of the placentæ; but that there is a further cause is indicated by the partial growth of the other side.

Whether these results point to the possibility of securing seedless tomatoes by reducing the amount of pollen employed, is questionable. In no case have we secured fruit when all pollen was excluded, and in every case the size of the fruit was in direct proportion to the amount of pollen used.

By careful selection we have secured tomatoes with relatively very few seeds; and Professor Bailey reports absolutely seedless fruits. # It is very doubtful, however, if these

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Rep. Cornell Univ. Exp. Sta. 1891, 55.

fruits can be regarded as anything but variations. The habit of the plant has become so modified that the influence of the pollen in stimulating growth is stronger than its fecundating power. In none of the plants bearing relatively seedless fruits, was there an apparent lack of pollen.

A further instance of a modified form of the fruit as a result of pollination was observed with the English cucumbers. As a rule, in cases of articifial pollination, if the fruit developed at all, the apex was much enlarged and perfect seeds were developed,— these seeds usually extending about one third the length of the fruit. This result I have found to be almost invariable with some varieties, — notably the "Telegraph", of which an example is shown in Figure 16.

Figure 16.

This peculiarity of form is the usual result of pollination in other varieties also; but it is not invariably the case, and Professor Bailey regards the irregular form as "an expression of plant variation, rather than a result of particular treatment." # Certain individuals may be more susceptible to the influence of pollen than others, but as the variation is traceable directly to the action of pollen in the impregnation of the ovules, the subject may properly be considered in this connection.

The reason for the failure of seeds to develop throughout the length of the ovary, in the long English cucumbers is as yet uncertain. It appears probable, however, that the explanation lies in the extreme length of the ovary and the consequent inability of the pollen tubes to penetrate so far. There has been a variation in the ovary without a corresponding variation in the pollen. The amount of pollen applied appears to have little effect in regard to this point.

In general, while little accurate work has been done in the way of determining the exact amount of pollen necessary for fertilization, it appears that the question has bearings of much practical importance. In some instances the size of the fruit seems to be in direct proportion to the amount of pollen used, while the form is much improved by an abundant supply. In some cases, on the other hand, fruits will develop without the intervention of the male element, and the best results are obtained when pollen is withheld.

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Bailey, Bul. 31, Cornell Univ. Exp. Sta., 137.

IV. ON THE GENERAL INFLUENCE OF FOREIGN POLLEN, AND OTHER MISCELLANEOUS OBSERVATIONS.

As already intimated, pollen appears in many cases to act directly on the ovary, stimulating growth of that organ independently of any effect on the ovules. This fact is most clearly seen in those species which do not readily cross.

In this connection, Focke remarks: "The pollen of the species acts quicker than foreign pollen and is alone effective if mixed with foreign pollen upon the stigma." ---------- "It is probable that if the pollen of the species is insufficient, foreign pollen may serve to develop the fruit, and thus serve a purpose." # Some instances strongly supporting this proposition have come under my observation. One of the large English cucumbers, "Duke of Edinburg" was given pollen of the "Emerald Gem" muskmelon. (In this case then, we have cucumis sativus crossed by cucumis melo). The cross was made in February. The resulting fruit attained about one half the usual size and then ceased growing. When the vines were torn from the house, in June, this fruit was still green while other fruits receiving pollen of the species two months later were fully mature. The ovules in the fruit in question were wholly undeveloped.

Two other instances of a similar nature were observed. The first of these was the common Summer Crookneck Squash crossed by the "American Turban" — Figure 17—; while the second was the same variety crossed by "Mammoth Tours" Pumpkin, — Figure 18.## In both of these cases the fruit developed, as indicated, about six inches in length, and remained in that condition several weeks.

A most remarkable instance of secondary influence of foreign pollen is that recorded by Lowe. ### Flowers of the yellow musk plant, Mimulus luteus were crossed with Mimulus Cashmerianus, which has spotted flowers. When the pods from these flowers were nearly matured, other flowers upon the same branches were given pollen of M. luteus. More than one hundred

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Die Pflanzen-Mischlinge, 448.

The two crosses last named were made by Professor L.H. Bailey at Cornell University. All other illustrations are from work performed by the writer.

E.J.Lowe, Rep. British Ass'n for Adv. of Sci., 1885, p.1087.

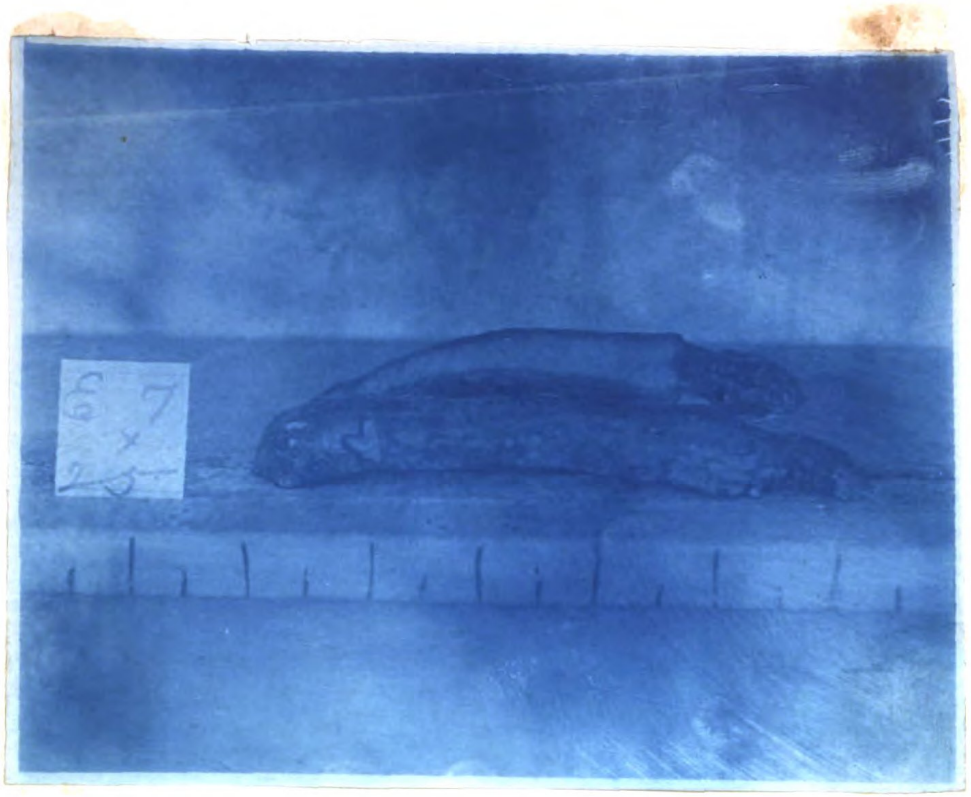

Figure 17.

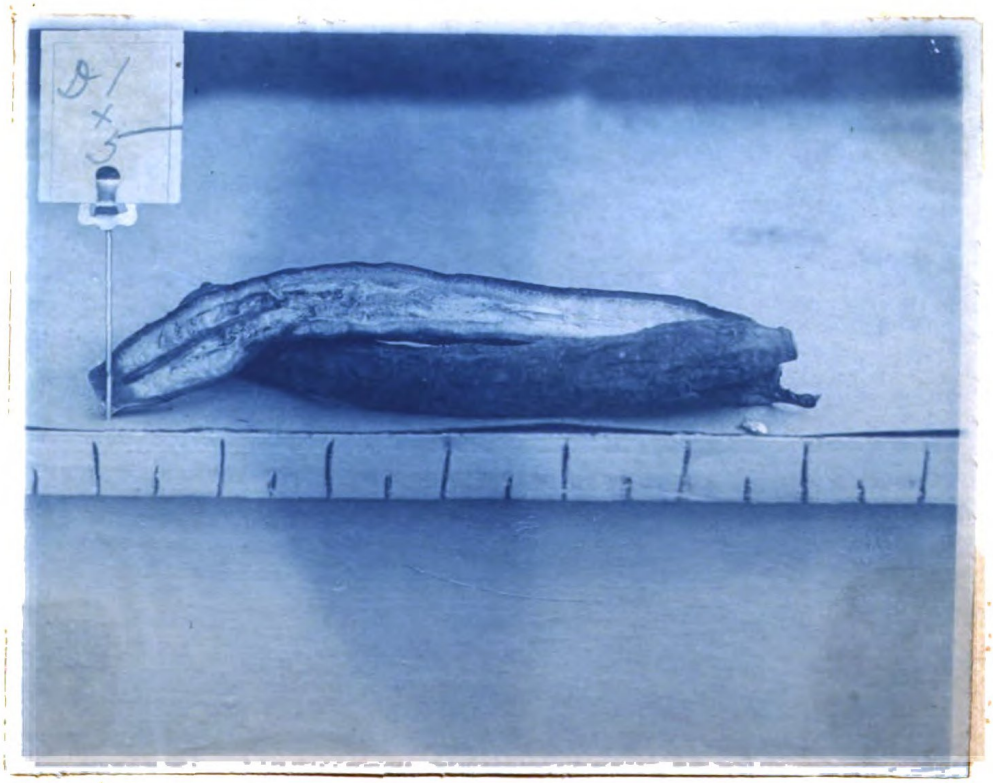

Figure 18.

seedlings were grown from these latter crosses and every one bore spotted flowers. In other words, the influence of the pollen of the foreign species was transferred along the branch and overcame the influence of pollen from the same species.

This result is in direct opposition to Focke's principle of the prepotency of pollen of the species as compared with foreign pollen, and as yet, so far as I am aware, Lowe's statements have not been verified. I have undertaken to prove the truth or falsity of the statements but have not as yet reached conclusions.

SUPERFŒTATION: Is it possible that the progeny of any plant may be in any way affected by the application of foreign pollen to the stigmas after self-fertilization has already taken place? Is it possible to obtain distinct effects from two male parents when the pollen is applied at different times? Comparatively little has been done toward solving these questions, and they are suggested as promising lines of investigation rather than as subjects for extended discussion at this time. Both Gray # and Focke ## have denied the possibility of superfœtation, but other observers have cited instances in support of the theory and certain facts have come within my own observation which point to the possibility of several seeds in the same ovary being the product of different male parentage.

Grieve in 1874 ### individually pollinated several blossoms on some plants of Pelargonium peltatum. One of these plants was on the day following given pollen of Pelargonium zonale. The offspring of the first plant were all true Pelargonium peltatum, while of the offspring of the second, no two were alike, the leaves of some being large and of others small; some showed a well developed zone, while others were without any indications of this character.

Charles Arnold in crossing corn, used pollen from both a yellow and a white variety on pistils of a dark purple sort. The resultant grains were yellow at the base and white at the top; while those of another ear on the same stalk, being individually pollinated, were of normal color.$ This instance established in the mind of Mr.Arnold the fact of the possibility of superfœtation, and was used by Thomas Meehan $$ as the basis for an argument in support of the theory of the immediate influ-

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\# Am. Jour. Sci. and Arts, XXV, 123.
Die Pflanzen-Mischlinge, 448.
Gard. Chron. N.S. Vol II, 689.
$ Gard. Month. XV, 104.
$$ Proc. Phil. Acad. Sci. 1873. 16.

ence of foreign pollen as well as of the theory of superfœtation.

In applying small amounts of pollen to the stigmas of tomatoes, I have observed that the portion of the stigma receiving pollen soon turned brown and withered, while the other side remained green and in an apparently receptive condition for some time. This fact was specially apparent in the fruit shown in Figure 14. As seeds develop only on the side receiving pollen, it seems probable that seeds on the other side of the ovary might well be fertilized by pollen of a different variety or species.

CONCLUSION.

Darwin, Wallace, Weismann and others have studied the laws of heredity, and have arrived at conclusions of vast importance in the systematic amelioration of plants. At the present time, however, but little is known of the laws controlling the numerous secondary results attending the crossing of plants. From the evidence at hand it appears that the secondary results may be of fully as much importance as are directly inherited qualities.

The collateral inheritance of qualities is by many absolutely denied, and there is much evidence in support of this position. There are instances, however, which strongly sustain the other side of the question, and it is probable that the truth lies between the two extremes.

That pollen has a direct stimulating effect on the ovary, independently of its action on the ovules, seems a well established fact. In many cases the size of the fruit is in direct proportion to the amount of pollen used; but it is also true that in many cases the fruit may develop to its normal size in the entire absence of the male element.

Whether superfœtation is possible, is a question of no small importance, but the evidence is as yet insufficient for conclusions to be drawn.

With all cultivated plants, however, there is an inherent tendency to revert to ancestral forms and this is a source of error to be guarded against in attributing certain results to fictitious causes.