

UNIVERSITY OF MISSOURI

COLLEGE OF AGRICULTURE

AGRICULTURAL EXPERIMENT STATION

RESEARCH BULLETIN 106

# Physiology of Reproduction in Horticultural Plants

II. The Physiological Basis of Intermittent Sterility with  
Special Reference to the Spider Flower

(Publication Authorized April 11, 1927)



COLUMBIA, MISSOURI

JUNE, 1927

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## II. The Physiological Basis of Intermittent Sterility with Special Reference to the Spider Flower\*

A. E. MURNEEK

ABSTRACT.—Spider flower plants (*Cleome spinosa*), grown in sand cultures with no external supply of nitrogen, and in soil cultures with a maximum supply of nitrogen, produced fruit intermittently. No marked effect of reproduction on rate of vegetative growth was observed except in nitrogen-low plants. The developing fruits were directly responsible for the initiation and maintenance of sterility in this plant. The non-fruited cycles were caused by a periodic abortion of pistils. By destroying the first fertile flowers, the spatial arrangement of the alternating sterile and fertile cycles could be interchanged. Periodic removal of the immature fruit pods caused a reduction and in some instances a total obliteration of the sterile male cycles. Abortion of female reproductive organs and hence sterility could be totally overcome by a continuous depistillation of all flowers. The effects of correlation between fruit and flower development may be localized in one-half of a diaxial plant. Sexual reproduction or gametic union is considered the primary cause of this mechanism, creating localized metabolic gradients to the detriment of other metabolically weaker parts of the plant. Some application of the results to the interpretation of particular types of sterility in horticultural plants is discussed. Suggestions are made of the comparative value of soil fertilization, pruning, and fruit thinning in obviating certain forms of sterility caused by overbearing of fruit trees.

### Introduction

Sterility in horticultural plants has long been recognized as not merely of theoretical interest, but important likewise in connection with commercial fruit growing. The proper setting and development of fruits and consequently the ultimate yield of an orchard is quite frequently limited by various types and degrees of sterility. Hence the subject has been studied diligently and extensively during the past twenty-five years. Still our interest in sterility, because of its importance, instead of diminishing seems to be increasing.

The results of numerous investigations in this field have emphasized the fact that sterility may manifest itself in diverse forms and that the cause or causes in most instances are very obscure. The various factors responsible for or associated with sterility in plants may be classified into (a) those external to the organism and (b) those of internal origin. Under the first category should be grouped all the diverse environmental factors to which a plant may be exposed. Trees growing in an orchard are naturally subject to an external environment which is largely beyond the control of man. The various cultural methods, such as fertilization

\*A summary of this investigation was presented under the title, "Correlation and Cyclic Sterility in *Cleome*," before the International Conference of Flower and Fruit Sterility, New York City, August 12-14, 1926.

and management of the soil, pruning, spraying, orchard heating, fruit thinning, etc., are, of course, directed according to the judgment of the fruit grower. Under certain conditions these practices may be so adjusted as to facilitate the highest degree of fruitfulness of an orchard. This, however, is true only in such cases where sexual reproduction and fruit development can be modified by controllable external factors.

It is satisfying to note that this has occurred rather frequently. Conspicuous and even striking increase in fruit setting has been secured, for instance, by the application of various fertilizers, particularly nitrogenous, at certain critical periods of growth and development of a plant. Likewise specific methods of soil management and particular types of training and pruning of trees has often resulted in a better set of fruits. In this respect we have by no means explored all the possibilities.

The second group of causal factors associated with sterility are commonly discussed under diverse topics, depending largely upon the point of view of the investigator. Inherent genetic influences, having their origin in the germplasm, apparently play a large, sometimes a dominating rôle. Generally the wider the constitutional hybridity, resulting from natural or artificial crossing, the greater the degree of sterility<sup>9, 4, 12, 19</sup>. There are many conspicuous exceptions to this rule, however, since narrowly bred varieties or strains may also be highly sterile<sup>13, 14, 23, 30</sup>.

While much convincing evidence has accumulated of late that many cases of inherited sterility may be interpreted on a simple Mendelian basis, there are other instances that apparently defy a genetic analysis<sup>31, 33, 34</sup>. Aside from some cursory observations on the inheritance of sterility in a few of our economic fruits, no careful and systematic investigation has been attempted in this field. The nature of the material and the time involved almost precludes an extensive inquiry into the genetic constitution of most of our tree fruits.

A commonly observed and a most popular form of sterility and unfruitfulness is incompatibility. Self-incompatibility is probably the most characteristic cause of self-sterility. The external reproductive organs of both sexes of the apparently perfect hermaphroditic flowers are normal, but they are non-functional *inter se*. This condition of sterility has been investigated by horticulturists through what may be termed the "manila bag method" more extensively than any other type. The results, while in a measure satisfactory from an economic standpoint, permitting more or less definite recommendations for interplanting of varieties have not been by any means uniform and conclusive. Some varieties in particular localities or in certain years must be considered but partly fertile. Moreover, in some orchards or fruit growing regions, or under certain climatic conditions, varieties known to be self-incom-

patible may fruit well without the presence of another variety. Evidently with most fruits self-incompatibility is but a relative and fluctuating condition, often so much so that the frequently employed term "partly fertile" has to be used as descriptive of the various intermediate states between complete self-sterility and self-fertility. Hence, after summarizing all the available information on the subject, Chandler<sup>7</sup> very logically concludes that "probably few varieties of fruits are self-incompatible to such a degree that they are self-sterile under all environmental conditions" and that "there seem to be varying degrees of self-incompatibility and that the degree of self-incompatibility may be influenced by environmental conditions." Thereby the study of sterility due to self-incompatibility seems to be reduced to and becomes largely a problem of physiology.

Another type of sterility expressed in various degrees of intensity is frequently caused by imperfections of floral organs, particularly parts closely associated with reproduction. Here belong also the interesting adaptations in flowers for the prevention of self-fertility, as exhibited by dichogamy and heterostyly of diverse kinds. If the suppression of sex organs is intense, plants may be permanently monoecious or dioecious.

Probably the most important and evidently the least observed alterations in sexuality are due to impotence of reproductive organs at various stages of development, including disturbances in gametogenesis. These morphological imperfections may vary from season to season, tree to tree, branch to branch, or even within the same branch. A true state of fluctuating intersexuality may thus exist, leading to intermittent fertility and fruitfulness. Such manifestations of sterility have been accepted by many as due to "evolutionary causes" or "tendencies"<sup>40,34,10,11</sup>. The direction of this tendency is assumed to be most often from a condition of normal hermaphroditism toward complete dioeciousness. Either sex may be involved.

This solution of the problem is as incongruous as it is sweeping. It is difficult to understand why this evolutionary change should be going on in some species, varieties, or particular plants and not in others. The use of a hypothetical expression, such as "evolutionary tendencies," really does not explain anything. It merely tends to cloak our lack of knowledge regarding the true nature of this phenomenon. Abortion and impotence of sex organs, being frequently of a fluctuating type, suggest at least that the underlying mechanism may be of a nutritional or physiological character.

The writer believes that the various states of sex intergrades and the resultant sterility offer an approach to a detailed study of not only this and related forms of sterility, but also the more puzzling type—

incompatibility. It is very likely that there exists not only morphological, but also physiological sex intergrades. Incompatibility may be but a less distinct, physiological manifestation, if one chooses to put it that way, of sexual impotence and intersexualism.

### REVIEW OF LITERATURE

The voluminous literature on the general occurrence and distribution of sex intergrades in higher plants has been ably surveyed and summarized by Yampolsky<sup>40,42</sup>, while changes of sex due to alterations in environment, specifically in nutrition, are quite fully discussed by Gardner<sup>16</sup>. Evidently variations in structure of reproductive organs, like those of other parts of the organism, are exhibited in all groups of plants. And floral morphogenesis may be influenced directly or indirectly by environmental conditions or cultural practices. Hand in hand with the increase of information on this subject has grown up an extensive terminology defining the main anatomical differences of various types of sex intergrades. No attempt is being made here to review all of the available literature on the subject. The necessary discussion is confined to publications that are germane to the problem in hand and deal more or less directly with horticultural plants of economic importance.

Although under normal circumstances most of our deciduous fruits form a really prodigious amount of pollen, not all of it is shed, and if distributed, may not be viable and potent. Numerous instances have been encountered of striking variations in structural development of stamens themselves and their total or partial inability to function as sex organs.

As early as 1902 Beach<sup>1</sup> and Booth<sup>2</sup> found that many American grapes produce various amounts of abortive stamens and non-viable pollen, and therefore are self-sterile. The degree of these imperfections and hence sterility, appeared to be of a changeable character even when the plants were in a normal state of fruiting. Environment may or may not have a direct bearing on the extent of sterility. Similarly, Dorsey<sup>11</sup> emphasizes the fact that in the grape abortive pollen was frequently associated with both sterile and fertile pollen. A detailed cytological investigation of the development of the male gametophyte showed that "sterile pollen in the grape results from degeneration processes in the generative nucleus or arrested development previous to mytosis in the microspore nucleus."

According to Reimer and Detjen<sup>28</sup> practically all cultivated varieties of *Vitis Rotundifolia* produce only pseudo-hermaphroditic flowers with reflexed stamens and defective pollen, while the only variety of

these grapes with seemingly perfect flowers, the Hope, in some years shows defective pistils, and is then unable to set fruit (Detjen<sup>8</sup>).

From a careful observation of a large number of varieties of grapes Stout<sup>32</sup> concludes that variations in morphological development of stamens and their ability to function as sex organs is due to various states of inter-sexualism of the blossoms. But within the same plant the stamens were found more uniform in structure than the pistils and "the intermixing of flowers of several types in the same cluster seemed to involve especially variations in the condition of the pistil."

That pollen viability is not a fixed state, but may be profoundly influenced by certain cultural practices which affect the plant more or less directly has been recently demonstrated by Winkler<sup>39</sup> with *Vinefera* grapes. Generally a less severe pruning than one usually given these grapes in California produced a striking increase in percentage of pollen germinating *in vitro*. With some varieties this increase was as much as six hundred per cent. An equally marked influence was noted in performance of pistils. Further discussion of this will be found on succeeding pages.

While the grapes have been investigated rather extensively in regard to pollen abortion and the mechanism analyzed in considerable detail, the phenomenon has been observed also in other fruits. Defective pollen seems to be a common characteristic in many blackberries (Brainerd and Peitersen<sup>4</sup>). In some varieties and pure species of American plums, though normal pollen development is typical, a certain amount of abortive grains are always present. And, according to Dorsey<sup>12</sup>, a large proportion of normal-appearing pollen fails to germinate when placed on receptive stigmas. Observations by Valleau<sup>36</sup> and others indicate that abortive stamens and defective pollen are commonly encountered in the strawberry, while Gardner<sup>16</sup> was able to change the Senator Dunlap variety, which normally bears perfect flowers, to pistillate by growing plants in pure sand. Similar evidence could be marshalled from citrus<sup>15</sup> and many other fruits of economic importance, all pointing to the fact that abnormalities in the male reproductive mechanism occur quite frequently.

Interesting and significant as this evidence of stamen and pollen abortion may be, of still greater importance are cases of sterility resulting from degeneration or abortion of certain parts of the pistil. Normally most deciduous fruits produce a large, often an enormous amount of pollen, which is usually carried by various agencies of pollination over considerable distances. Hence, though a great proportion of the stamens should be defective and much of the pollen impotent even to a point where many of the plants show complete functional femalehood,

still a high degree of fertilization and fruitfulness may be and frequently is maintained. Not so when a considerable number of pistils are defective. To insure a profitable crop of fruit in an orchard, a comparatively high percentage of pistils, ovules and eggs necessarily must be normal and functional. This does not seem to be always prevailing even with our popular varieties.

Some early observations by Lord<sup>25</sup>, Goff<sup>18</sup> and Waugh<sup>37,38</sup> on abnormalities in pistil development in plums are of much interest. Considering several varieties of native plums (*P. Americana* and *P. nigra*), Lord says that they "produce more or less blossoms without pistils; and on some trees and even groups of trees none of the blossoms ever have pistils and, of course, bear no fruit." and "what is more peculiar, some trees will bear fruit for a series of years and then for a year or perhaps more than one year, the blossoms will be without pistils." Goff, too, noted a high percentage of defective pistils in a number of American plums, particularly on one-year-old wood. An extensive inquiry into the problem of plum pollination by Waugh disclosed the fact that surprisingly large numbers of abnormal pistils may appear on all varieties. A summary of two years' observations with different groups of plums shows that defective pistils may run from 4.3 per cent in the *Domestica* group to as high as 21.2 per cent in *Americana*. It should be pointed out that these figures are averages. The range in the three major groups was estimated as follows: European plums, 0-45%; Japanese plums, 0-73%; *Americana* plums, 0-100%.

Moreover, an analysis of blossoms of the Burbank and other varieties collected from different parts of the country showed clearly that within the same variety the extent of pistil abnormality may show marked variations. This must not be interpreted as the result of a direct effect of the external environment, but rather as due to differences in the internal physiological state of the trees from which these flowers were gathered. Waugh himself points to age and health of the tree and storage of reserve substances as some of the important factors bringing about abortion of the female reproductive organs. Corroborating these deductions he quotes<sup>37</sup> Munson as saying that: "it seems impossible with present data to find any constant connection between defectiveness of pistils and conditions of soil, cultivation or climate. The pistils may be defective in one year and sound the next." This is in close agreement with the views of Stout<sup>32</sup> that the physical character of pistils of American grapes may vary from year to year.

Waugh refers to a seedling plum, which as a consequence of the bearing of a heavy crop, became so exhausted that in the following year



it did not produce a single perfect blossom. A similar situation is described by Hendrickson<sup>21</sup>. A French prune tree, which was induced to set an abnormally heavy crop, the next year had not only fewer blossoms, but the percentage of those setting was smaller, and in general the flowers were weak in appearance and function. A suggestive generalization of his is that "the performance of this individual tree may be taken as an example of what may possibly happen in an entire orchard if the trees are overloaded by increased pollination."

Systematic studies of sterility in the American plums have led Dorsey<sup>12</sup> to the conviction that it may be interpreted on the basis of "different factor combinations" bringing about a condition of arrested development of pistils, ovules or embryos. On the other hand, in discussing the first drop of fruits, which is usually caused by pistil degeneration, he says that, "the occurrence of so many aborted pistils in seasons following heavy fruit crops suggests a connection with nutrition," adding that "if this assumption is correct, a small degree of abortion may be interpreted as suggesting a competition between different flowers in a bud, while a total abortion indicates a much more general condition." That competition among flowers for the available food supply may be a factor is indicated by the results of Miss Bradbury<sup>3</sup> who obtained an increase from 24 to 42 per cent in fruit setting of the sour cherry when the blossoms were thinned to one per cluster, while the existence of a more general correlation between nutrition and pistil abortion is clearly shown by Winkler's recent work<sup>20</sup>.

By decreasing the amount of pruning Winkler was able to increase the number of berries per cluster in several *Vinifera* grapes. This was particularly feasible when both pruning and the crop were reduced ("part crop"). It is of significance that with non-pruned vines an inverse correlation was observed between the number of berries per cluster and the size of the crop. Thus non-pruned "part crop" Muscat of Alexander bore on the average  $119 \pm 2.1$  and  $140 \pm 2.5$  berries per cluster during two respective years, but only  $58 \pm 1.9$  and  $57 \pm 2.9$  berries on non-pruned "all crop" vines. When compared with normally pruned grapes, the increase on the non-pruned was 266 per cent in the case of a part crop and 62 per cent with a full crop. This seems to point quite certainly to an increasing competition for the available food supply with increasing numbers of flowers and fruit. A comparison of leaf area of variously pruned vines, bearing either a full or a part crop, and the efficiency in flower performance seems to indicate that these differences may be accounted for on a nutritional basis. Thus the ratio between number of leaves and viability of pollen or set of normal berries remained rather constant as the following figures show:

|                              | Normal Pruning | Half-long pruning (part crop) | Cane pruning (part crop) |
|------------------------------|----------------|-------------------------------|--------------------------|
| Leaves/berries               | 6.5            | 6.7                           | 7.2                      |
| Leaves/germination of pollen | 42.8           | 44.7                          | 42.6                     |

It would be of further interest to know to what extent an increase in efficiency of both the male and female organs in these instances was due to various methods of pruning and the concomitant changes in leaf area and to what degree it may have been caused by differences in the amount of fruit matured by these vines.

That the morphological development and functional capacity of pistils may be determined sometimes by the effects of correlation between the developing fruit and flowers may be gleaned from an extensive investigation of sterility in the strawberry by Valteau<sup>36</sup>. As the flowering season of the strawberry progressed a marked decrease in fertility was observed in blossoms produced in succession on the branching flower stalks. This was clearly shown by the formation of increasingly large numbers of irregularly shaped fruit and by complete sterility and unfruitfulness of some of the blossoms. A positive correlation was found to exist between flower position and fertility of pistils and flower position and size and number of carpels per fruit. But "a comparison of the pollen condition in the flowers born on various positions", says Valteau, "shows that pollen abortion is in no way related to flower position and thus to dioeciousness, as are the various anther types and sterile pistils."

The following summary from a table by Valteau indicating the general relationship between flower position and number of fruit set in hermaphroditic and pistillate varieties of strawberries is worth examining:

TABLE 1.—RELATIONSHIP BETWEEN FLOWER POSITION AND NUMBER OF FRUITS SET IN HERMAPHRODITIC AND PISTILLATE VARIETIES OF STRAWBERRIES—VALLEAU.

| No. of varieties      | No. of stalks examined | Position of flowers on stalk |         |           |         |          |         |            |         |         |         |
|-----------------------|------------------------|------------------------------|---------|-----------|---------|----------|---------|------------|---------|---------|---------|
|                       |                        | Primary                      |         | Secondary |         | Tertiary |         | Quaternary |         | Quinary |         |
|                       |                        | set                          | not set | set       | not set | set      | not set | set        | not set | set     | not set |
| <b>Hermaphroditic</b> |                        |                              |         |           |         |          |         |            |         |         |         |
| 10                    | 400                    | 452                          | 6       | 800       | 107     | 685      | 356     | 81         | 155     | 1       | 5       |
| Percentage            |                        | 98.7                         | 1.3     | 88.2      | 11.8    | 65.8     | 34.2    | 34.3       | 65.7    | 16.6    | 83.3    |
| <b>Pistillate—4</b>   |                        |                              |         |           |         |          |         |            |         |         |         |
| Percentage            | 128                    | 158                          | --      | 286       | 29      | 177      | 89      | 90         | 80      | --      | 6       |
|                       |                        | 100                          | --      | 90.8      | 9.2     | 66.5     | 33.5    | 52.9       | 47.1    | --      | 100     |

These results show unmistakably a conspicuous increase in sterility from the first to the last blossom in both types of plants. This relationship held true when the flowers were bagged and selfed, though the percentage of set on all plants was smaller.

An analogous observation has been made by Schuster<sup>35</sup> on the Ettersburg No. 121 strawberry. In this variety almost all of the primary blossoms formed fruit when artificially pollinated, while only 13 per cent of secondary blossoms set. This was true whether the plants were selfed, cross-pollinated or open-pollinated. Secondary blossoms that did not set appeared to have normal stamens and pistils, though the number of pistils per blossom was considerably smaller than in primary flowers.

Valleau attempts to explain his results on an evolutionary basis by supposing that the cultivated hermaphroditic and pistillate forms of the strawberry have been derived from males of the wild strawberries, "which exhibit a high percentage of their low fertility in the primary flowers." It can be more safely assumed that the maturing fruit on the subtending axis of the stalk is the direct cause of the increasing sterility of the subsequently developing flowers.

This has actually been demonstrated by Gardner<sup>16</sup>, who by a timely removal of the primary, secondary and tertiary flowers of the cluster was able to obtain a relatively high percentage of setting of the later blossoms, which normally would be sterile. Such deflorated flower clusters matured as many berries as untreated plants, but the fruit was smaller in size and hence the yield correspondingly reduced.

Gardner made a series of tests on the effect of nutrition on sex expression in the strawberry wherefrom he concludes that "the interesting point in this connection is that flower abortion is not greatly influenced by extremes of nutritive conditions in the soil and in plants at the time of fruit bud formation" and that "spring fertilizing had practically no influence on the percentage of flowers that aborted." The evidence pointed to the fact "that nutritive conditions within the strawberry plant at the time of fruit setting are of considerable importance in influencing the setting of the flowers."

A rather varied yet periodic manifestation of sterility leading to intermittent fruit production has been found and carefully discussed by Stout<sup>33</sup>. In several strains of two species of the Chinese cabbage (*B. pekinensis* and *B. chinensis*) three distinct types of sterility were noted during the period of flowering: (a) Impotence, manifesting itself in arrested development or abortion of flowers. (b) Proliferation of pistils, due most likely to unusual vegetative vigor. (c) Physiological incompatibility of various grades of intensity, but exhibiting a distinct periodicity and, as a rule, the highest degree of self-compatibility during the period of mid-bloom. Pedigree cultures showed that self-compatibility in these plants was not a hereditary character.

Evidently all of these types of sterility could be associated with alterations in vegetative and reproductive vigor of the plant. Their appear-

ance was distinctly cyclic and coordinated among the different branches. Hence the phenomenon was very suggestive as having not only a physiological basis, but also a physiological coordination. Stout believes that "the various types of sterility in these species of *Brassica* decidedly indicate a mutually limiting relationship between vegetative and reproductive vigor."

Another type of cyclic sterility of somewhat different and very interesting character may be commonly observed in the spider flower, *Cleome spinosa*. This vigorous annual produces fruit intermittently (Fig. 9). It is sterile only as far as it is fruitless. Many controlled pollinations by Stout<sup>24</sup> showed no physiological incompatibility in all instances where the sex organs were developed normally. There is, however, a periodic reduction in size and structure of both stamens and pistils, which during the course of the sterile cycle exhibit many morphological grades of intersexes (Fig. 11). If not extremely reduced, stamens may produce viable pollen and may be functional. Aborted or rudimentary pistils, on the contrary, always fail to set seed. Alternations in sexuality and fruitfulness could not be correlated by Stout with changes in external environment nor with the general vegetative vigor of the plants. He, therefore, concludes that cyclic fruitfulness in the spider flower is most likely due to internal biogenetic regulation and is possibly directed by specific stimulating or inhibiting influences.

Somewhat similar periodicity in fruit setting has been noted in the Hubbard squash (*C. maxima*) by Bushnell<sup>6</sup>, who says that "a proportion of the first flowers produced will not develop into fruit under most favorable conditions." This appeared to be entirely independent of the external environment. As no measurable differences could be found between the essential organs of fruitful and non-fruitful flowers, physiological periodicity evidently exists in the pistillate flowers of this robust vine.

While studying the fruiting habit and pollination of cantaloupes, Rosa<sup>29</sup> observed two or possibly three cycles of fruitfulness under the environmental conditions at Davis and Turlock, California. The various branches (spurs), though functioning to some extent as independent units, are considerably synchronized in respect to fruit setting as the following table shows:

TABLE 2.—CANTALOUPE FRUIT SET AND DEVELOPED ON DIFFERENT SPURS—ROSA

| Spur No.             | 1  | 2  | 3  | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|----------------------|----|----|----|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|
| Number set.          | 14 | 12 | 9  | 6 | 4 | 4 | 4 | 5 | 7 | 7  | 10 | 6  | 9  | 4  | 4  | 4  | 2  | 0  |
| Number developed     | 13 | 5  | 7  | 1 | 0 | 0 | 1 | 0 | 1 | 3  | 7  | 4  | 2  | 0  | 0  | 0  | 0  | 0  |
| Percentage developed | 42 | 16 | 22 | 3 | 0 | 0 | 3 | 0 | 3 | 10 | 22 | 13 | 7  | 0  | 0  | 0  | 0  | 0  |

Rosa describes the periodicity in fruit setting of the cantaloupe as follows: "The different branches of the plant form the fruit of this crown

set (the set of fruits on the first spurs of each branch) at very nearly the same time—during the period of not over one week. Following it is a period of two or three weeks during which few if any fruits are set, then comes a more or less indefinite period when setting may occur again, with a second period of non-setting following it, and possibly a third of setting still later on." The foregoing table shows distinctly two fruitful and two non-fruitful cycles.

Nipping of branches at the time when the eighth spur was blossoming did not seem to destroy the cyclic condition of fruitfulness, but apparently was conducive to "an increased tendency toward setting and development of fruit on the later spurs (the beginning of the second fertile cycle), though this may not be entirely due to the effect of nipping."

This seems to suggest that in the cantaloupe there is apparently either a weak correlation or none at all between vegetative extension and fruitfulness, but rather between the developing fruit of the preceding fertile cycle and morphogenesis of the succeeding flowers. Here then is exhibited a phenomenon which is quite similar to intermittent fruitfulness in the spider flower, *Cleome spinosa*.

#### MATERIAL AND METHODS

The present investigation was initiated as a result of the writer's interest in the spider flower as a favorable material and the analysis of cyclic sterility as a means of approach to studies of the physiological basis of certain forms of sterility in horticultural plants. Particular emphasis has been placed on the possible causes of pistil abortion—a conspicuous feature in this plant during the sterile cycles.

All of the specimens used for experimental purposes were raised in late winter and early spring from seed collected at random. Several series of plants were grown in containers of twelve-liter capacity in a standard greenhouse environment (Fig. 8.) To obviate any disturbances that might result from secondary vegetative growth, the plants were trained to a uniaxial type of development. This is easily accomplished by the prompt removal of all side shoots.

Throughout these investigations attention was centered upon two questions: (a) What is the general influence of nutrition on cyclic manifestation of fruitfulness? (b) What, if any, are the effects of correlation between the developing fruit and sex expression of the succeeding flowers?

In studies of nutrition of plants nitrogen has commonly been found a most potent and effective limiting factor. Hence several groups of plants were grown on two levels of nitrogen supply. A few series were raised in pure quartz sand, which was watered from time to time with a weak nutrient solution, minus nitrogen, and of the following proportional composition:  $MgSO_4$ —2%,  $KH_2PO_4$ —2%,  $KCl$ —1%,  $CaCl_2$ —4% and

$\text{CaSO}_4$ —2%. Other series were supplied with a complete nutrient medium which had the relative composition of  $\text{MgSO}_4$ —2%,  $\text{KH}_2\text{PO}_4$ —2%,  $\text{KNO}_3$ —2%,  $\text{CaCl}_2$ —3%,  $\text{CaSO}_4$ —2% and  $\text{Ca}(\text{NO}_3)_2$ —4%.

Though the complete nutrient solution, when diluted with six volumes of tap water, is very satisfactory for growing tomatoes<sup>26,27</sup>, it appeared to be unadaptable for the spider flower. Practically all specimens in this medium developed a chlorotic condition in the young leaves. This disturbance in chlorophyll formation could be overcome neither by various adjustments in the proportion of the salts nor by addition of inorganic or organic iron compounds. Even spraying of the leaves with weak solutions of iron salts did not have any effect on chlorosis. It is of interest to note that a liberal addition of  $\text{KNO}_3$  to the minus nitrogen cultures gave rise to somewhat similar chlorosis of the terminal growth. This difficulty necessitated the growing of plants of the nitrogen plus series in a rich garden compost, which was watered at frequent intervals with a dilute solution of  $\text{NaNO}_3$  and  $\text{KNO}_3$ . Thus normal plants of two desirable somewhat extreme types of growth were finally secured. Those in sand cultures without nitrogen were weakly vegetative (Fig. 10). Others in rich soil, plus nitrates, were high in nitrogen and very vigorous (Fig. 8). The two groups will be referred to hereafter as "nitrogen low" and "nitrogen high" plants.

A certain stage in development having been reached, plants of both series changed from a vegetative to a reproductive state. Those in sand cultures preceded the soil series in blossoming by about thirty days. All open flowers were pollinated daily by transferring with finger tips pollen collected at random to all receptive stigmas. It is thought that a high degree of fertilization was accomplished by this practice.

The rate of growth of all plants, based on increase in height, was measured at weekly intervals from a fixed point at the base to the tip of the stem. The development and behavior of each plant, but especially of all floral organs, was recorded either once or twice during every twenty-four hours. Comparative observations were made also on plants grown outdoors.

To learn of the possible effects of correlation between the developing fruit, vegetative growth and morphogenesis of floral organs, the following experimental treatments were performed on several separate series:

1. Flower buds were removed continuously.
2. A number of flowers corresponding to the average number in the first (fertile) cycle were cut before opening.
3. Half-mature fruit pods were harvested at certain intervals.
4. All pistils were pinched off soon after opening of the flowers.

## RESULTS

Although this investigation extended over a period of one year only, it included several series of plants grown under natural and controlled conditions. The conclusions presented here are from observation of well over 10,000 flowers, the development and behavior of 8,638 of which has been carefully recorded. Hence the results are thought to be quite typical.

**Effects of Reproduction on Vegetative Growth.**—In recent studies with the tomato the writer has demonstrated (Murneek<sup>26, 27</sup>) that reproduction, when at a maximum, has a decidedly retarding effect on vegetative development. The tomato, however, is a plant with a more or less continuous type of growth. With normal development, when no inhibition prevails, vegetation and reproduction progress simultaneously. In fact, a certain amount of vegetative growth is a necessary precursor for flower formation. The spider flower, on the contrary, shows no continuous growth. Once sexual reproduction is initiated on any of the vegetative axes, flower production becomes incessant. To be sure, ordinarily vegetative vigor to a certain extent overlaps reproductive activities in this plant. A number of secondary shoots usually develop from some of the nodes. Their most rapid growth may be simultaneous with the flowering of the central stem. These lateral branches likewise terminate in flower production, which remains uninterrupted till the end of the season.

As stated elsewhere, all plants used for the present experiments were trained to a single stem. Flowering having once begun, all the activities of these plants were confined to reproduction. This condition in every instance was maintained till termination of the experiments, the total period being approximately as long as the normal length of life of this annual.

The blossoms of the spider flower are arranged raceme-like on a vegetative axis. It was of interest to learn to what extent, if any, the linear increase of this stem or peduncle is correlated with or guided by the developing flowers and fruit. Hence at set intervals a careful measurement was made of the rate of elongation of all plants, beginning with the time they had become established in the permanent cultures. The summarized results of these measurements are presented in graphic form in Figs. 1 and 2.

It is seen that in the case of nitrogen-low plants of the sand culture series there is a distinct break in all of the curves, corresponding with the onset of the reproductive phase or the flowering period. In control plants marked "normal", this occurs considerably earlier than in other groups and the decline in rate of growth is more marked. Nitrogen most likely

acting as a limiting factor in these cultures, the developing fruit of the control plants naturally absorbed and incorporated into the seeds all that was available in storage form in the plant proper. Yellowing and dropping of leaves was a conspicuous feature of this series, nitrogen being absorbed from these organs and translocated to the fruits. All the leaves having been lost in this manner, the stem in turn was cleaned of its reserves, resulting in the death of the whole plant, excepting the

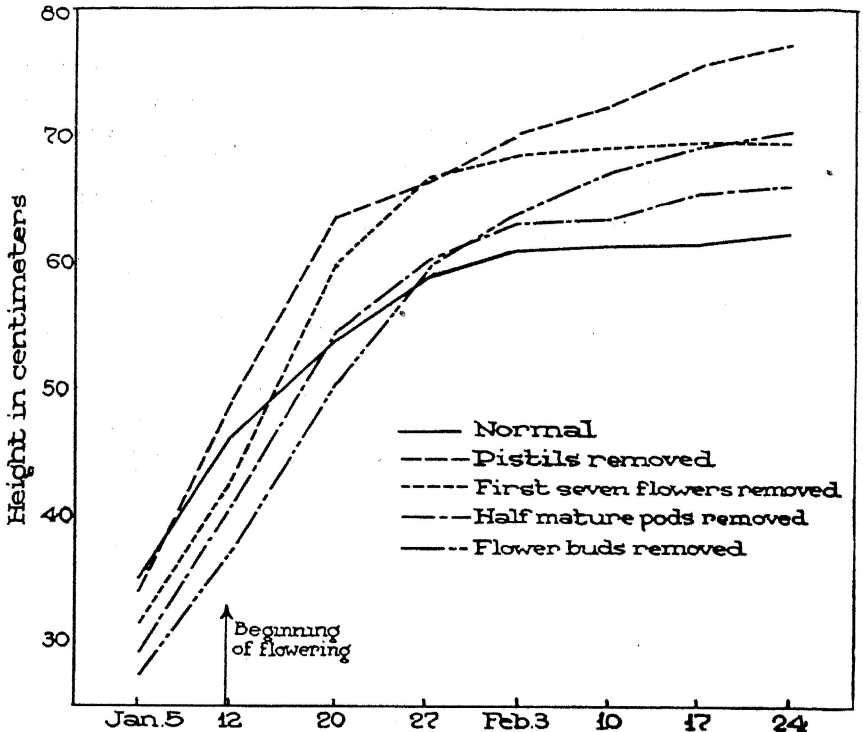


Fig. 1.—Rate of growth of nitrogen-low plants.

seeds. Naturally before this stage was reached flower development had ceased.

That the maturing fruit and seeds were directly responsible for this early curtailment in growth, is clearly evident when the graph expressing rate of growth of normal plants is compared with those of the depistillated ("pistil removed") and the deflorated ("flower buds removed") series. Curves representing the latter groups are so much alike that they can be almost superimposed. They differ from that of the control plants in showing neither so distinct a break with onset of flowering nor so definite a decline toward the end of the season.



On the other hand, when the first seven flowers were removed, which normally would have set fruit, or when half mature pods were cut periodically, the plants attained a greater height. The conspicuous decline in rate of development in this group began later than in control plants,

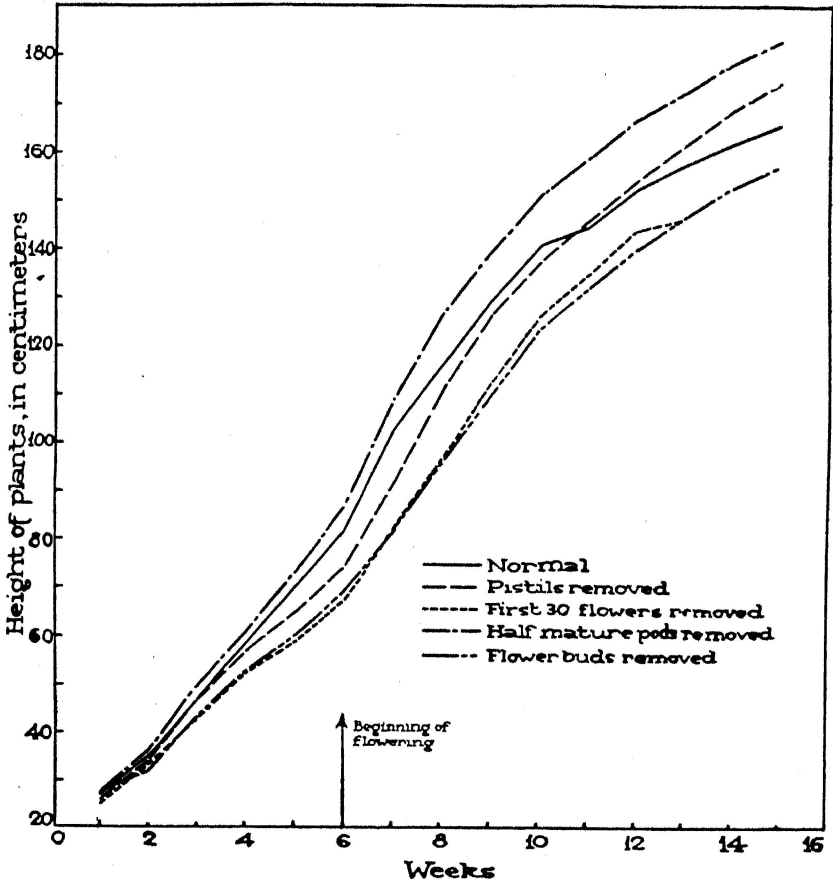


Fig. 2—Rate of growth of nitrogen-high plants.

since in the first instance development of fruit began later and in the second, as a result of cutting of the half mature pods, exhaustion due to ripening of seeds was prevented.

This evidence points unmistakably to the effects of correlation between the developing fruit and seeds and the rate of vegetative extension under the conditions of a very limited nitrogen supply. An entirely different picture, however, was exhibited by plants grown with a very ample supply of nitrogen, and no limitation in other nutrient elements, as in the present soil series (Figure 2.)

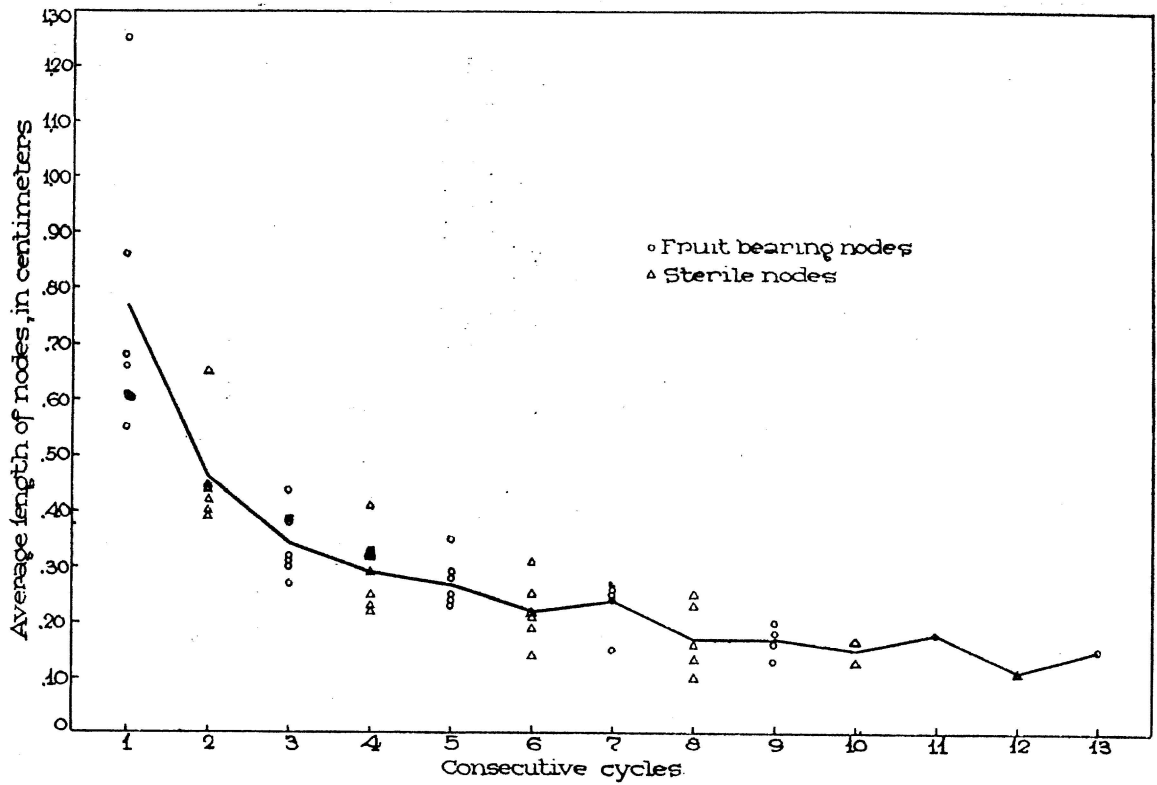


Fig. 3.—Seasonal changes in length of fruit bearing and sterile nodes.

The graphs representing rate of growth of all groups of the nitrogen-high series run quite closely together. There is no indication of a general decline in vegetative vigor, except towards the very end of the season, and then only in the control ("normal") plants and those from which the first thirty flowers were removed. With an ample supply of soil nutrients, particularly nitrogen, naturally one would not expect a retarding effect in growth of the stem as a result of the developing fruit, if it is remembered that the many sterile flowers that normally occur on these plants probably precluded a *maximum* state of reproduction. The gradual reduction in growth during the end of the season should be explained on the basis of a declining vigor. This may have resulted largely from the progressive destruction of the photosynthetic mechanism due to the successive abscission of leaves from the basal region of these plants.

The rather conspicuous bend occurring in practically all of the curves at the time of flowering and pointing to an accelerated rate of growth is worth noting (Figure 2). This may have been caused by purely accidental changes in such environmental factors as were not under direct control in this investigation, particularly light and heat. But since this abrupt change occurs exactly at the time of flowering, it probably may have come about from the effects of stimulation due to fertilization (gametic union). If this is the true explanation, then we have here examples of increased metabolism analogous to what was found in the tomato<sup>27</sup>. Still a similar acceleration, though somewhat less conspicuous, occurred likewise in plants from which flower buds were removed before anthesis, and thus fertilization was precluded. Hence one is thrown back to environmental factors as a most likely cause or to a second possible alternative. Stimulation in metabolism may have taken place coincident with the formation and development of flowers and gametes, this being separated from the secondary stimulation secured from gametic union<sup>27</sup>. Speculative as this may appear, recent convincing disclosure of the existence of a female sex hormone in plants and its possible distribution beyond the organs of reproduction (Loewe et al. <sup>24</sup>), makes this probable.

In order to secure a still closer picture of the possible effects of reproduction on associated vegetative tissues, numerous measurements were made of the average length of fruit bearing and sterile nodes throughout the region of flower formation. The material for this analysis was obtained from plants grown outdoors.

The results presented in Fig. 3 show practically no difference in length between fertile and sterile nodes. The slight fluctuations toward the end of the season may be accounted for on other basis than the effects

of the appended fruit. There is, however, a distinct seasonal decrease in length of all nodes.

**Effects of Fruit on Flower Development.**—Environmental factors, particularly soil nutrients, have often been found quite potent in altering the development of sex organs and their normal function. When the spider flower plant is grown without an external supply of nitrogen, as in the present sand cultures, sterility, though differing in intensity, is still of a cyclic character. In about ten per cent of all individuals the first cycle consisted of staminate flowers, which naturally were non-fruitful. Otherwise the cycles began as usual with hermaphroditic flowers, then changed to male, to hermaphrodite, etc. (Figs. 4-A and 10.)

It should be made clear at this point that, while the reproductive organs of both sexes showed distinct morphological abortion, limitations to fruitfulness were brought about only from abortion of pistils (Fig. 11). All aborted pistils were non-fruitful and sterile. There was always plenty of viable pollen available for fertilization. It should be understood, however, that occasional aborted and rudimentary stamens most likely produced various amounts of non-viable pollen (Stout<sup>34</sup>). This condition was not determined. The alternating cycles are spoken of as consisting of male and of hermaphroditic flowers, since stamens always produced some pollen and never set limitations to fruitfulness. Hence by "male" or "staminate" flowers are understood here any blossoms the pistils of which were non-functional but the stamens produced and shed pollen whether all of the pollen grains were viable or not.

From a large number of counts it was quite clear that staminate flowers predominated in the nitrogen-low series. Moreover, the last blossoms on these plants were either males or highly reduced females. The most conspicuous effect on sex expression resulting from lack of nitrogen was a general increase in maleness. The distinctly cyclic production of fruit was not changed to any marked degree.

When approximately 30-35 blossoms had been formed on these plants, further flowering ceased. To be sure some buds were still found, but these turned yellow and abscised before opening. This, of course, was an unmistakable sign of loss of vigor, a consequence of the developing fruit; for as soon as pods of the first cycle had matured and released their contents of seeds, normal opening of buds recommenced, provided the whole organism had not become too far exhausted.

It was thought of value to know to what extent, if any, the positions of the alternating cycles might be shifted by the removal of the first few flowers. Consequently from groups of plants the first seven blossoms corresponding to the average number in the first fertile cycle were cut before opening. In practically all instances such plants, instead of forming

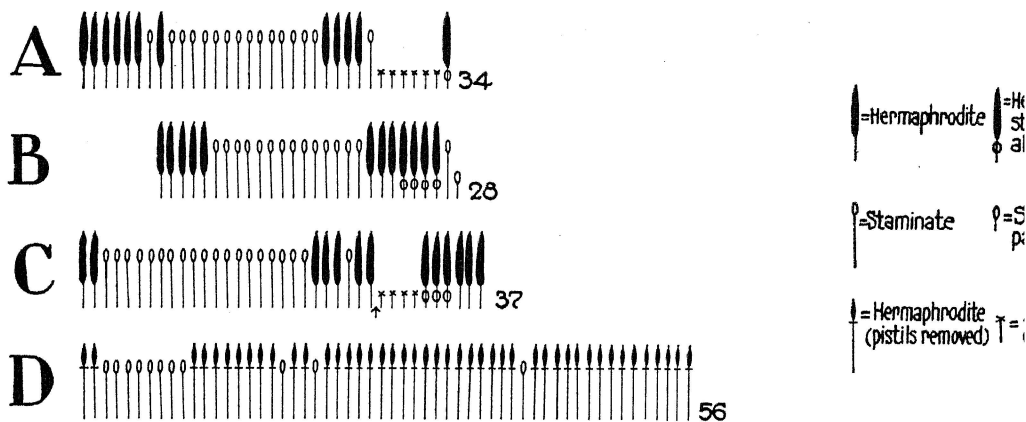


Fig. 4.—Chart illustrating a typical sequence of various blossoms on normal and treated nitrogen-low plants. A. Control (normal). B. First seven flowers removed. C. Half-mature pods removed (at arrow). D. Pistils removed continuously. Figures indicate average number of flowers per plant.

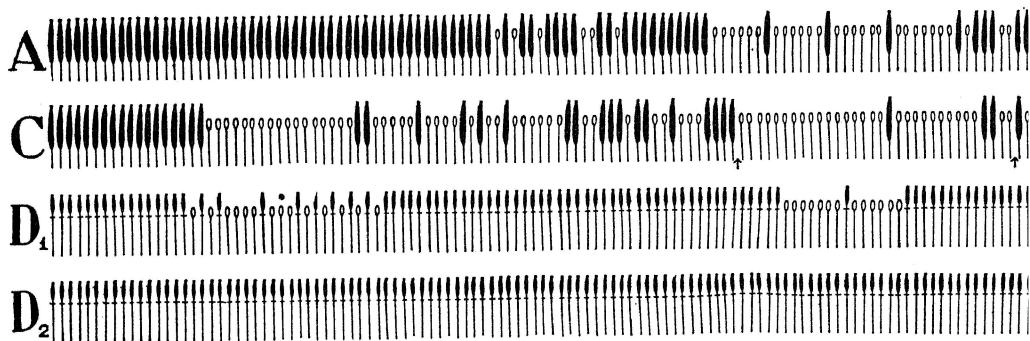


Fig. 5.—Chart illustrating a typical sequence of various blossoms or what slo

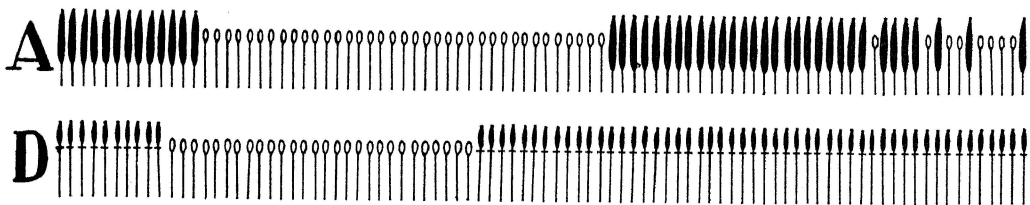
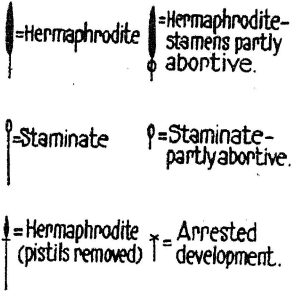
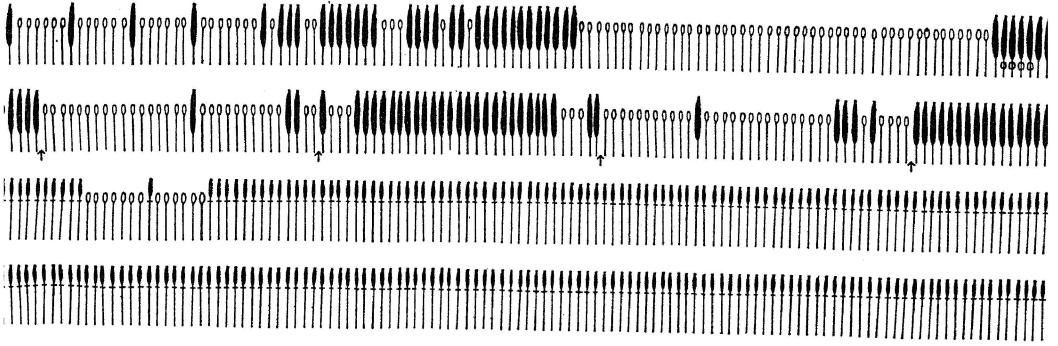


Fig. 6.—Chart illustrating a typical sequence of various blossoms on control and treated branches of tw branch. For legend to symbols see Fig. 4.

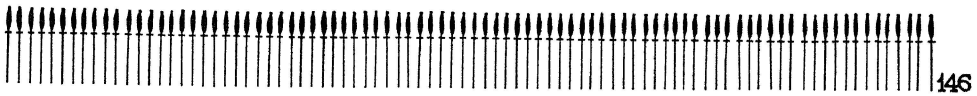
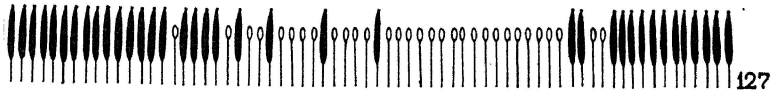


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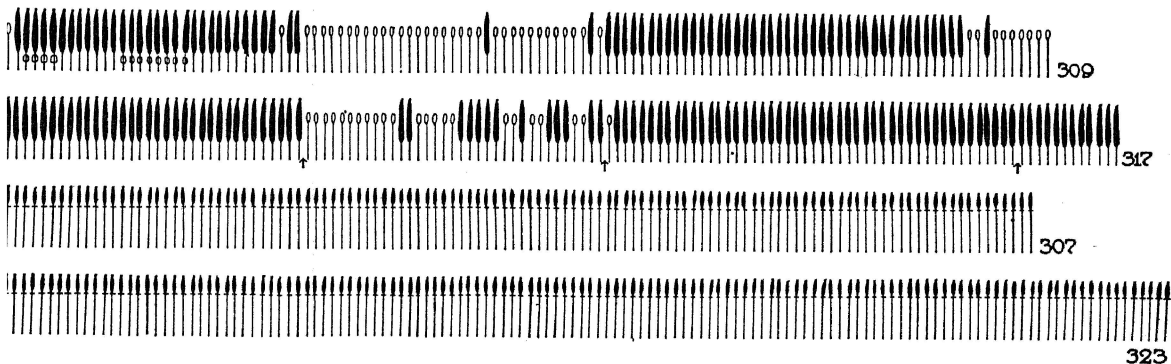
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cal sequence of various blossoms on normal and treated nitrogen-high plants. A. Control (normal). C. Half-mat what slow. D<sub>2</sub>. Pistils removed continuously—response immediate. For legend to :



control and treated branches of two-stemmed plants. A. Control branch. D. Depistilled legend to symbols see Fig. 4.



alf-mature pods removed (at arrows). D<sub>1</sub> Pistils removed continuously—response some-  
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staminate flowers in this position, produced perfectly normal and fertile hermaphrodites. (See Fig. 4-B.) This made it quite clear that the spatial arrangement of flowers was not unchangeable. Moreover, the behavior of these and of the control plants pointed unmistakably to the effects of correlation between the developing fruit and sex expression in the succeeding flowers.

To learn still further of the function of this mechanism, the first fruits were removed when about half grown, as judged by size (Fig. 12-B). Under this treatment in the nitrogen-low group of plants, recovery from the usual inhibition due to fruiting was prompt if the pods had not attained too high a stage of maturity (Fig. 4-C). When more or less mature pods were removed, recovery proceeded slowly and was incomplete. A few specimens had become so far exhausted by the maturing of the first crop of fruit that no recovery was obtained. Such individuals most likely had utilized all of the available or bound nitrogen, as indicated by the abscission of practically all leaves. This condition resembles closely a similar response by the tomato when grown without an external supply of nitrogen<sup>26</sup>.

To complete the evidence, one more step was required. Consequently from other groups of plants all pistils were cut immediately after opening of the flowers (Fig 12). This led to a shortening of the first cycle of sterile or staminate blossoms and a reduction of the second and third cycles of males to a single, rarely two blossoms. Following this an uninterrupted production of hermaphroditic flowers was initiated, which continued till the plants reached a stage of complete devitalization (Fig. 4-D.) In many specimens of nitrogen-low plants under this treatment but one short cycle of male flowers was formed, the rest being perfect.

This situation existing when plants were growing in a medium devoid of nitrogen, it was naturally of great interest to find whether intermittent appearance of sterile flowers could not be overcome by a liberal or excessive feeding with nitrogen. With this object in view the maximum tolerance for nitrogen by the spider flower was carefully ascertained by successive additions of this element in the form of weak solutions of  $\text{NaNO}_3$  and  $\text{KNO}_3$ .

The rather typical results are presented in Fig. 5-A. In every case reproduction in these nitrogen high and very vegetative plants began with highly functional hermaphroditic flowers of the usual size for *Cleome*. The first 7-50 blossoms had normal stamens and pistils. No sooner the first fruit pods began to develop, then this cycle was followed by a somewhat shorter group of staminate flowers, next a group of complete flowers again staminate, etc. (Fig. 5-A.) The majority of blossoms were hermaphrodites. In spite of the very ample supply of nutrients, especially nitrog-



enous, this series behaved very much like plants normally grown outdoors (Fig. 9). Intermittent sterility due to pistil abortion was clear cut and definite.

A periodic removal of immature pods from nitrogen-high plants was accompanied by a shortening of the cycles of staminate flowers very much as in the minus nitrogen series (Fig. 5-C). In some instances this caused a complete change from intermittent to continuous production of perfect flowers, which were highly functional both as males and females. Thus it was unmistakably demonstrated that *the developing fruits were directly responsible for the initiation and maintenance of sterility in the spider flower* and that *this mechanism could not be shifted to any appreciable degree by drastic changes in the nutrient level.*

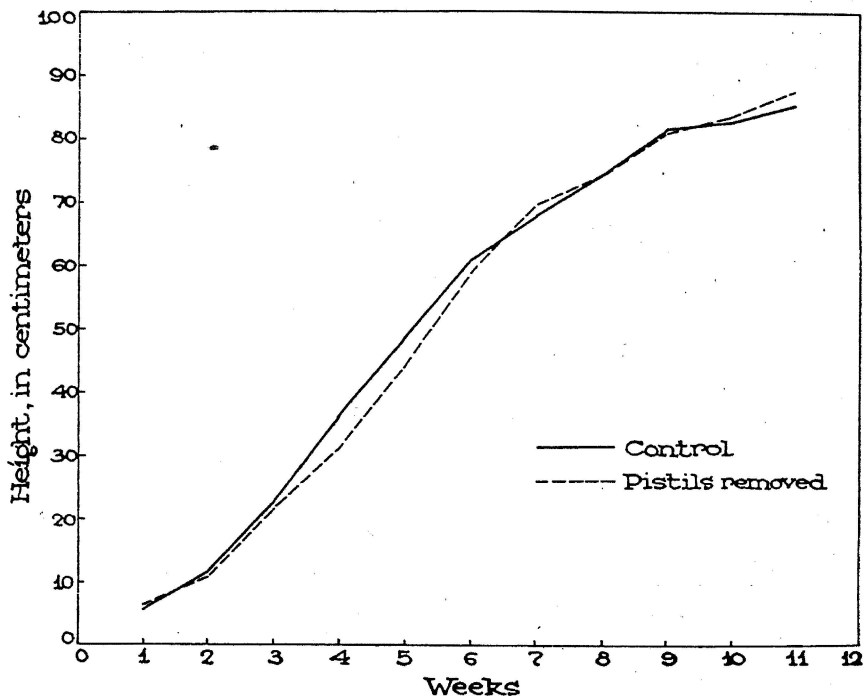


Fig. 7.—Rate of growth of control and treated branches of two-stemmed plants.

When fruit development was prevented in these extremely vigorous plants by a prompt removal of all pistils, one or two abbreviated cycles of sterile flowers still appeared. Then a rapid change from a condition of cyclic sterility to one of complete fruitfulness could be observed. Soon an uninterrupted succession of perfect flowers was produced without the slightest manifestation of the characteristic periodic alternation to maleness (Fig. 5-D<sub>1</sub>). Moreover, in fully fifty per cent of specimens in

this group complete hermaphroditism and hence continuous fruitfulness was induced from the very beginning by daily removal of pistils (Fig 13). Not a single staminate flower was obtained during the growing season. Many of these plants were permitted to form more than 300 flowers—all hermaphrodites. (Fig. 5-D<sub>2</sub>). When fruit was allowed to develop, the usual cyclic condition of sterility was readily initiated.

To make it more certain that variation in sex expression in the spider flower is not of an inherent but purely nutritional and correlative character, a number of plants of the soil or nitrogen-high series were trained to a diaxial type of growth. Such two-stemmed plants are easily secured by an early removal of all lateral growth excepting at two desired points. The main stem was cut off above these side shoots. One of the branches on each plant was left undisturbed, producing fruit periodically. Pistils were removed from the second in a manner detailed above.

The results in every instance were as if two individual plants had been employed for the experiment. The depistillated half of each plant exhibited the characteristic inhibition of staminate cycles. After some time only perfect flowers were formed on the treated branch (Fig. 6-D); while during the same period the normal and control branch showed the usual intermittent alternation in sexuality and fruitfulness (Figs. 6-A and 14). Hence it seems quite certain that *the effects of correlation between fruit and flower development are more or less localized.*

The rate of growth of the two branches of such artificially produced dichotomous plants, as measured from the point of their union and expressed in weekly increments in height, is presented in Fig. 7. Practically no difference in elongation of the two branches can be observed.

## DISCUSSION AND APPLICATION

The current discussion of the results obtained from this investigation is limited to their general bearing on the nature of certain forms of sterility in horticultural plants of economic importance. A brief consideration of some salient points of theoretical significance will be found elsewhere (see footnote, page 3). A few of these perforce must be referred to here also.

Sterility due to imperfections or abortion of the male or female reproductive organs has been commonly explained either on the basis of an "evolutionary tendency" or else an unfavorable effect of the external environment, particularly the general state of nutrition of a plant. The former conception implies an inherent state, which is largely beyond control, unless the causal mechanism is disclosed. In its present setting, this conception appears to be merely an assumption and a generalization, not an explanation.

External factors, however, particularly when expressed through the general state of nutrition—the internal environment—seem to have a distinct significance here. Excessively vigorous as well as extremely devitalized plants may produce defective sex organs<sup>39,16,37,33</sup>. In the present investigation, for example, it was shown that alternation in sex expression may be brought about to some extent at least by drastic changes in the supply of nitrogenous nutrients. Still in a large number of cases it has not been possible to establish a definite relationship between the various environmental factors and pistil or stamen abortion<sup>16,1,37,34,6,29</sup>. In this respect, however, a connection, though existing, may not be always obvious.

It is likely that sex organs, because of their higher metabolism, may be more delicately adjusted to or influenced by at least some factors of nutrition than the vegetative parts. Hence plants of apparently equal vegetative vigor may show striking differences in reproductive activities. The tomato plant, for instance, when induced to bear a maximum crop of fruit, will exhibit certain characteristic changes in development: First an inhibition of fertility, then decrease in size of floral organs, and finally a conspicuous reduction in vegetative development<sup>26</sup>. Moreover, the female sex organs, due to their terminal position and nature of tissues involved, may have a higher metabolic gradient and therefore very probably require proportionally larger amounts of various vital substances, especially nitrogen<sup>17,5,16</sup>. Consequently any disturbances in metabolism that may arise will affect the pistils more readily than the stamens, leading to one-sided sterility and unfruitfulness. Such general reactions by the reproductive organs may or may not have a parallel expression in other strictly vegetative parts of a plant.

A specific state of nutrition, however, does not depend solely upon the external environment. Under more or less identical conditions two individuals may behave in strikingly unlike manner, depending very largely upon their comparative reproductive activities—the formation and development of seeds and fruit. To illustrate: A bearing tomato plant will develop and function very differently than one not permitted to develop fruit, though both may be growing side by side in the same container. The influence of reproduction and fruit development on the general metabolism may be very marked indeed. So much so that even a drastic shift in the intensity of external factors or levels of nutrient supply will not neutralize the effects of correlation between reproductive and vegetative functions, in the tomato at least, provided fertilization and seed production is kept at a maximum.

A somewhat different but equally effective type of correlation is exhibited by the spider flower, a plant with determinate development but

progressive flowering. As stated before, correlation here may be largely between the developing fruit and morphogenesis of the succeeding flowers. When a proportionally large crop of seeds or fruit is developing on any axis of this plant, the following flowers will show periodically subnormal structure, pistil abortion being the most conspicuous feature. As a consequence the long raceme-like inflorescences exhibit recurring cycles of sterility. To be sure, at times stamens also may be found abortive, particularly in their capacity to form viable pollen. This, however, in no way affects the general state of fertility in this plant.

A most interesting and characteristic feature resulting from this investigation was the impossibility of destroying this correlation by subjecting the plants to extreme conditions of nitrogen nutrition, which ordinarily is a most potent way of modifying the general developmental processes in plants. Yet by the simple practice of cutting the immature fruit pods, the sterile cycles were markedly shortened, and by preventing the setting of fruit through continuous removal of pistils, sterility could be completely overcome. Thus in the behavior of the spider flower, like in the tomato, we have a vivid illustration of the striking influence of sexual reproduction on metabolism.

That the effects of correlation between the maturing fruit and flower development are in a measure localized, is evident from the behavior of two-stemmed plants. In this respect, too, there is a close parallel between the spider flower and the tomato. Moreover, it supplies additional proof that the mechanism of correlation has its seat in the fruit and seeds and that the results are due largely if not entirely to diversion of the available food supply to the developing fruit. Once a large enough number of pods have set, certain substances apparently are monopolized to such an extent that little will be at the disposal of the adjacent flowers. The pistils being the more sensitive organs, they naturally will respond most readily to a restricted supply of nutrients. In general, *sexual reproduction or gametic union may be considered the key to this situation, creating localized metabolic gradients to the detriment of other metabolically weaker parts of the plant.*

These results suggest a number of points of application to horticultural practice. Under favorable circumstances many of our fruit trees, for example, often overbear, and as a consequence not only the fruit will be small in size and poor in quality, but the tree will become so devitalized that the development of flowers for the following season will not proceed normally. With excessive yields of fruit the very initiation of flower primordia may be curtailed, bringing about biennial bearing with all its concomitant undesirable features. With lighter crops and hence less exhaustion, flowers may be formed, but they will be relatively

small and weak<sup>21,26</sup>. Even blossoms of normal size under these circumstances may exhibit various degrees of abortion of pistils and stamens<sup>1,2,32,25,37,38,39</sup>. Such flowers are incapable of performing their functions in sexual reproduction and hence are sterile. In this respect a tree may behave as a unit or the various branches<sup>22</sup> or even spurs<sup>20,22</sup> may show considerable individual differences, depending largely upon the degree and extent of exhaustion.

It is very likely that, with fruit trees in certain states of nutrition, the relationship between yield of fruit and food supply, particularly organic, may be such that though flowers may be produced, which appear structurally normal, they will not function properly. Hence the effects of correlation between fruit and flower development can be expressed not only on a morphological, but also on a physiological basis. In this relationship, too, either sex may be involved. To quote Yampolsky<sup>41</sup>: "We may have as many physiologically intergrading conditions of sex as there are morphologically intergrading sexes."

Looking at the situation from this point of view, all such cases of self-incompatibility among our cultivated fruit varieties that apparently are not due to genetic or environmental factors may be caused more or less directly by the effects of the previous crop on flower performance in the succeeding year. This in a measure would explain the inconsistencies in the degree of self-sterility that have been secured with practically all of our fruits that have been investigated extensively enough<sup>7</sup>.

To overcome these undesirable types of sterility, two means appear to be available to the fruit grower. If the condition is of rather general and not too intensive nature, a careful attention to the improvement of vigor of the tree by proper practices in soil management, fertilization and pruning may be very helpful. Incidentally this explains why the application of nitrogenous fertilizers during certain critical periods has given such remarkable results in increasing the set of fruit. Likewise systematic pruning causing more or less localized stimulation may have very beneficial effects. But in order that the proper remedy may be applied, it appears to be highly desirable to know the exact internal state of nutrition of the tree in each instance. The most feasible way of obtaining a true picture would be by chemical analysis for various essential substances were it not so cumbersome. As an alternative the rate of growth of twigs and spurs and the character and appearance of foliage may be used for diagnostic purposes as indicative of the general vitality of the plant. In every instance vegetative development should be correlated with the previous yield of fruit.

The most logical and surest remedy, however, is a proper regulation of the size of the crop that a tree may be permitted to bear without detri-

mental effects on its future performance. This is of particular importance not only with perennial plants, but also with such annuals that have an indeterminate type of development. In this respect fruit thinning suggests itself as the most natural procedure. In commercial practice, however, most of our deciduous fruits are thinned so late that the expected benefit to the tree does not always materialize. We have yet to work out a method of thinning flowers or else fruits early in their development.

Judicious pruning seems to be another and very practical means of regulating and adjusting the crop in accordance with the vitality and capacity of the tree. But in order that pruning may produce the desired results, it should be detailed, so called "fine pruning." Under some circumstances "spur pruning" could be used most effectively. Detailed pruning in a large measure may be considered a good substitute for fruit thinning.

Considering our small fruits, but particularly the grape, pruning appears to be an especially valuable method of so adjusting the crop that the greatest efficiency in normal reproductive functions may be expected under particular states of growth and development. Likewise with vegetables and flowers of indeterminate growth, the fruit should be removed as early as possible if a maximum crop is to be expected. This procedure, of course, must be adjusted within the limits of commercial practice. Under no circumstances should such plants be allowed to mature fruit or seeds early in the season, if their commercial value be negligible then but profitable later on. And to obviate the initiation and development of cyclic sterility in many of our trailing plants—cantaloupes, cucumbers, squashes, etc.—systematic thinning of the fruit may be found of marked benefit.

In general then, fruiting of a plant is a devitalizing process. A maximum crop of fruit and seeds under existing conditions, though not necessarily the largest in volume; will most certainly lead to grave disturbances in the future performance of a plant, a conspicuous feature of which is abortion and sterility of the sexual organs. An adjustment of the crop to the capacity of the machinery for food production is the natural remedy.

### SUMMARY

1. Spider flower plants grown in sand cultures with no external supply of nitrogen and in soil cultures with a maximum supply of nitrogen produced fruit intermittently.
2. A minimum amount of nitrogen did not effect this periodicity except by a slight increase in the total number of male flowers.
3. The non-fruiting sterile cycles were caused by a periodic abor-

tion of pistils. Flowers on each raceme were alternately males and hermaphrodites. Abnormalities in stamen development, though sometimes present, did not influence the general state of fertility.

4. No marked effect of reproduction on vegetative growth was observed except in nitrogen-low plants. In these instances very likely nitrogen acted as a limiting factor, most of it being absorbed and incorporated into the maturing seeds and fruit.

5. A removal of all of the first fertile flowers changed male blossoms of the second normally sterile cycle to perfect hermaphrodites. Thereby the spatial arrangement of the alternating groups was interchanged.

6. Periodic cutting of the immature fruit pods led to reduction in the number of blossoms of the sterile staminate groups. In nitrogen-low plants this treatment caused also an extension of the flowering period, while in nitrogen-high plants it permitted a more or less continuous fertility during the later part of the season.

7. When pistils were cut promptly, thus preventing the formation of fruit, male flowers were reduced in numbers and consequently sterility became gradually less evident. Finally only perfect blossoms were formed on these plants. In many specimens of the nitrogen-high groups depistillation caused from the start a continuous production of hermaphroditic flowers. When fruit was allowed to develop, cyclic sterility was again initiated.

8. The effects of correlation between fruit and flower development may be localized to one-half of a diaxial plant. Under experimental treatment each branch of such two-stemmed plants behaved as a separate individual. The mechanism of correlation appears to be initiated by and localized primarily to the reproductive organs.

9. Some application of the results to the interpretation of particular types of sterility in horticultural plants is discussed. Suggestions are made of the comparative value of soil fertilization, pruning, and fruit thinning in obviating certain forms of sterility resulting from overbearing of fruit trees.

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Fig. 8.—A part of the experimental cultures showing nitrogen-high plants. Note size of plants as compared with average stature of a student.



Fig. 9.—Racemes of plants grown outdoors, showing characteristic cycles of fruitful and sterile flowers. Pods on lower half have dehisced.



Fig. 10.—Typical plants of the nitrogen-low series. Plant “a”—normal (control).  
Plant “b”—depistillated. Heights comparable.

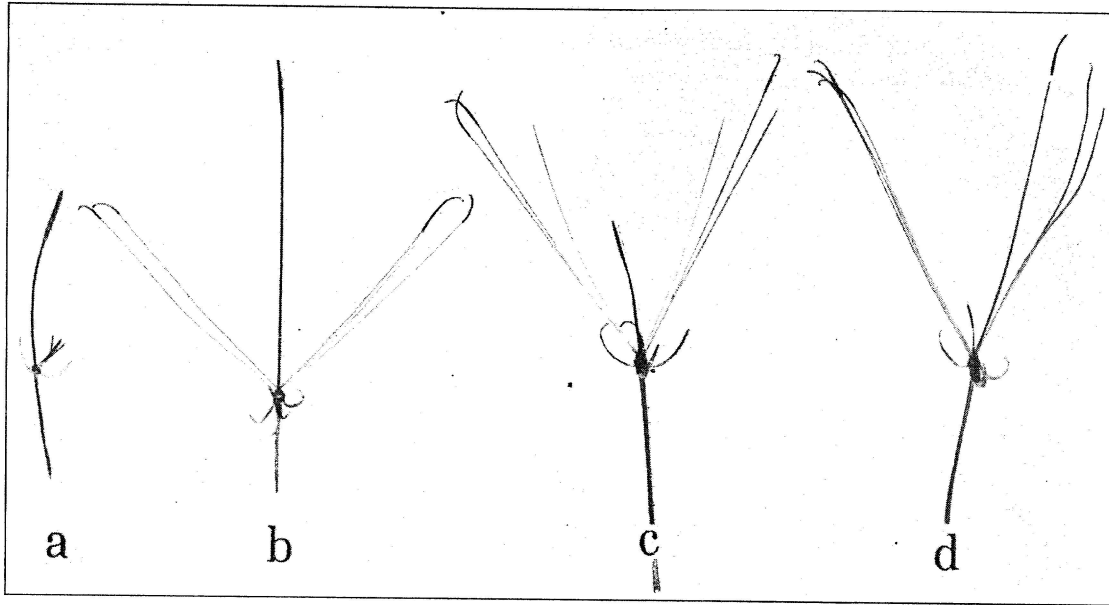


Fig. 11.—Flowers showing characteristic abortion of pistils and stamens. Flower "b"—a normal functional hermaphrodite. "c" and "d" illustrate various degrees of pistil abortion—both non-fruitful. "a" is a typical reduced flower, occurring in small numbers toward the end of life on nitrogen-low plants.

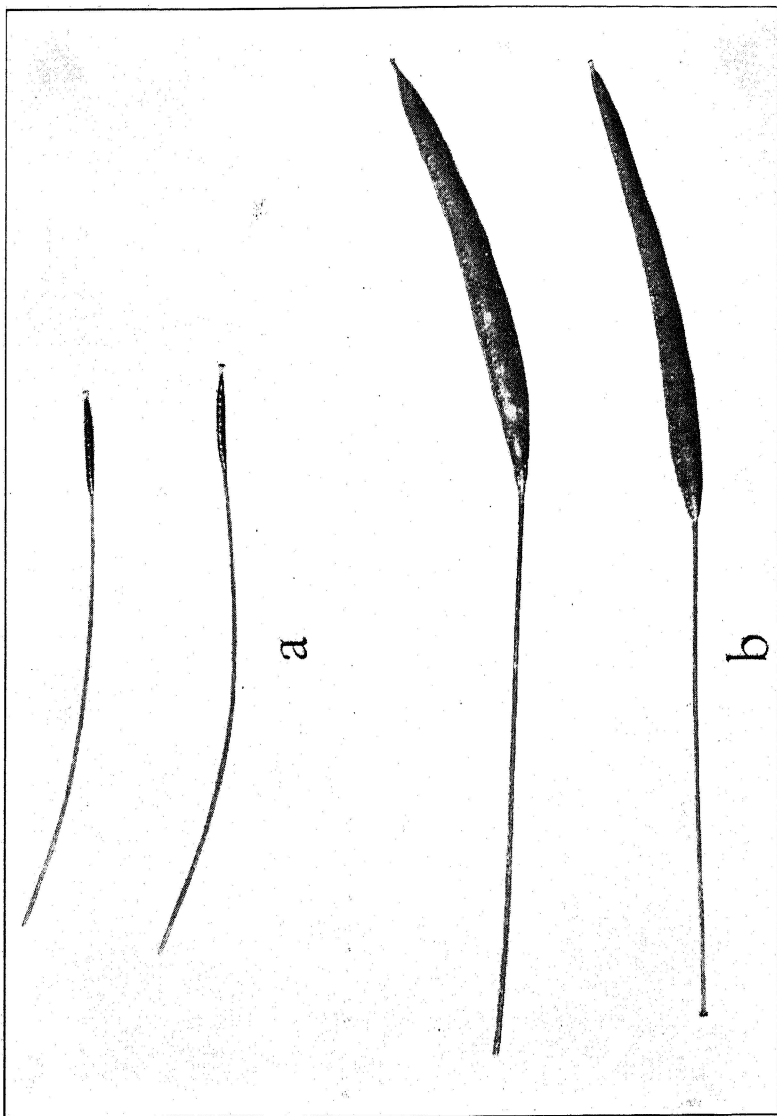


Fig. 12.—Pistils at time of fertilization (a). Half-mature pods at time of cutting (b).

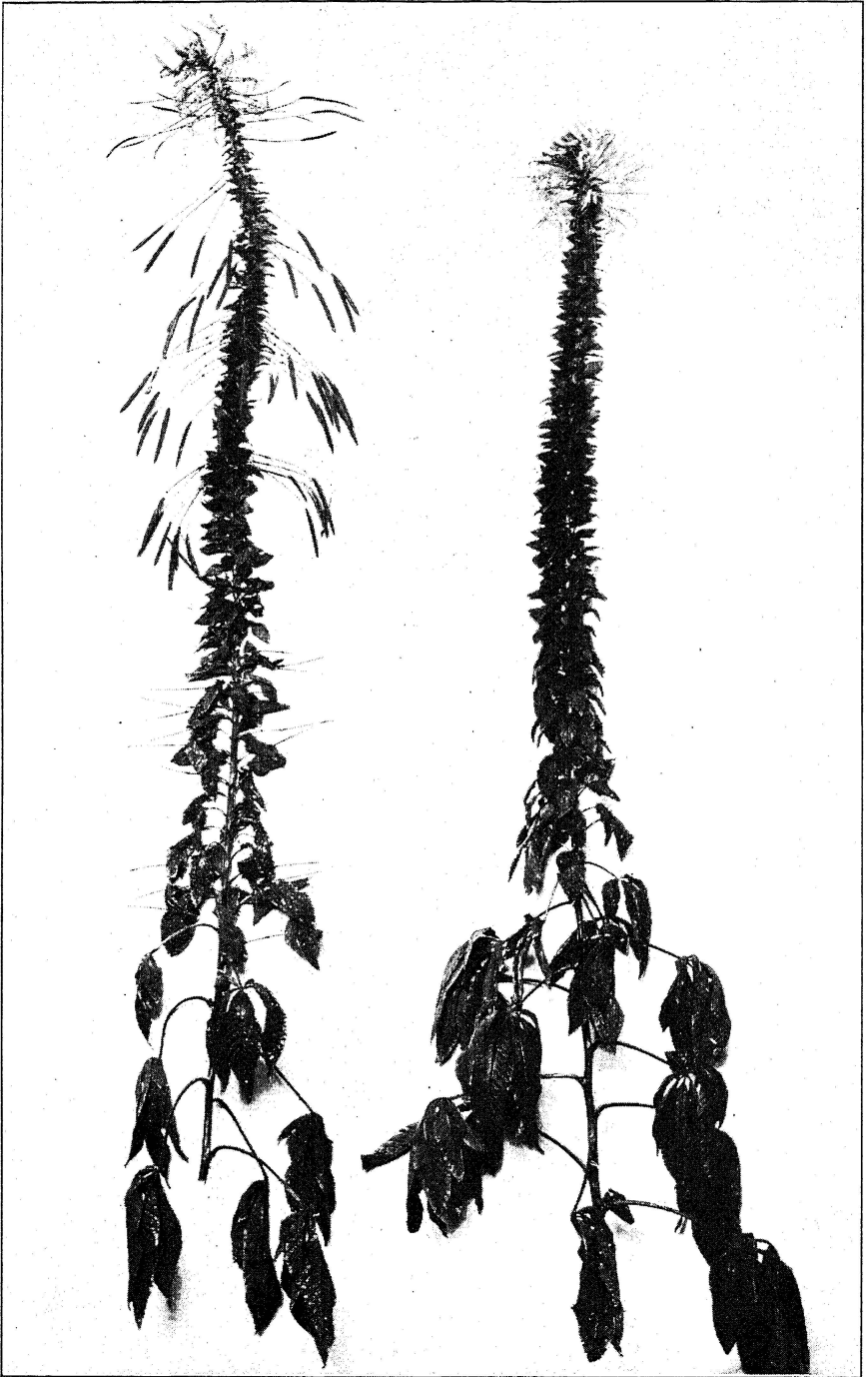


Fig. 13.—Plants grown with an ample supply of nitrogen. At the left is a typical control plant. At right a depistillated plant, which produced perfect flowers continuously.



Fig. 14.—A two-stemmed plant. By daily removal of pistils branch "a" was induced to form perfect flowers continuously. Control branch (b) at the same time showed alternating cycles of sterile and fertile blossoms.