Irregularities in the formation of reproductive organs, such as are seen in the phenomena of intersexualism in both plants and animals, have two points of special interest. First, they involve a particular type of sterility of various grades and degrees of expression, which in plants often affects the production of fruit and seeds and becomes a matter of practical importance in respect to crop production and in the breeding of various economic plants. A second point of interest is in the bearing which the phenomena of intersexualism have on questions of sex differentiation, the alternation of sex, and the evolutionary tendencies in reproduction.

In its general significance, several points regarding sterility from intersexualism are clear. In plants it tends to the alternative development of one or the other kind of sex organs, giving, in comparison to the fundamental condition of hermaphroditism, a one-sided sterility. There is incomplete development or abortion of one or the other of the sex organs which is discriminating and which results in alternative development, with, however, many grades in the relative development. Thus, in plants, the so-called “sterile” intersexes are, in general, individuals that are predominantly male and often highly functional as such. These individuals are sterile only in the sense that they are fruitless. Also the so-called “self-sterile” individuals and varieties of plants, as is well shown in the cultivated grapes in which sterility from intersexualism is well marked, are predominantly female and able to function feebly or not at all as males. They are productive of fruit only when properly pollinated from male or hermaphroditic individuals. Very seldom, if ever, is complete sexual impotence for a plant as a whole seen as a condition of intersexualism, as is frequently the case in sterility from hybridity.

But in many cases of intersexualism in animals, to which attention has recently been especially directed, the complete sterility of individuals is very frequent. Here, however, the condition arises in dioecious forms and involves the partial change of an organ from one sex to the other after

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differentiation has been partly achieved. This often results in a more or less complete sexual impotence or sterilization, a condition which has naturally been very generally regarded as abnormal and pathological. This is, however, not the case in those species of plants which are prevailing dioecious or monoecious, for here, as well shown in the muskmelons, there is a tendency to produce flowers that are fully functional as hermaphrodites.

Whether, however, intersexualism results in complete sterility, as it frequently does in dioecious animals, or in one-sided sterility, as is the rule in hermaphroditic plants, the physiological basis for these variations in sex is to be regarded as most fundamental in the determination and expression of sex.

It is, furthermore, to be recognized that the mixture of sexes, with blending and changes in the character of the organs, often results in a wide range of variation in the morphological character of the different sex organs produced by a single individual. In many plants, the flowers on a single individual may be staminate, pistillate, and hermaphroditic, with also many intergrading types, thus exhibiting many grades of sexual impotence with marked differences in the ability to produce fruit.

These cases of partial variability in sex are of special interest, for here the various conditions of alternative impotence with corresponding irregularities in the production of fruit are all seen among the flowers of a single individual. In such cases there is also opportunity to observe whether the variations are irregular and sporadic or whether they are related to a definite period in development or are otherwise periodic. It is with special reference to these questions that the changes in the character of the flowers of Cleome spinosa L. are here reported as decidedly alternative and repeatedly cyclic, resulting in the intermittent production of fruit.

Observations on Cleome spinosa

This species is most favorable material for a study of variation in the sex of flowers in relation to the development of the plant as a whole. It has long been known as having mixed flowers, yet the species has not become dioecious. All the individuals of the species are apparently quite alike in respect to the general range of variations in the sex of the flowers. The species is a quick-growing herbaceous annual. The first flowers open on the main raceme when the plant is relatively small—about two feet tall—and while the lateral branches are scarcely visible. The main raceme continues to elongate, producing flowers daily, often for a period of from eight to twelve weeks. Meanwhile a dozen or more lateral branches develop, and these may in turn branch. All the branches grow rapidly and produce flowers in abundance. When autumn arrives, well-grown plants are five or more feet tall with a spread of branches of as many feet in diameter. There has been a long period of bloom, often covering as many as ninety days, and this has been for the most part coincident with the period of
rapid vegetative development. By far the greater amount of the vegetative growth of the plant takes place after the blooming begins. The first fruits are ripe and shed their seeds when the plant is only about half grown. The period of vegetative vigor overlaps that of the flowering and reproductive vigor in a decided degree and to an extent seldom seen in plants. Only during the last few days of bloom do vegetative growth and vigor noticeably wane.

Fig. 1. Main raceme of a plant of Cleome spinosa at the close of the blooming period, showing the intermittent production of fruit. This raceme was about 3½ feet long. The pods on the lower half have dehisced.

At the close of the growth of the plant, about September 15th to October 5th as grown at the New York Botanical Garden, the main branch of a plant from the point where the flowers are first produced appears as shown
in figure 1, the raceme being about three feet in length. Lateral branches are similar but frequently somewhat shorter. It is to be noted that the pods are in groups separated by sections of the stem upon which no fruit was formed. Fruit formation is therefore decidedly intermittent.

This habit of producing fruit intermittently was observed by the writer in groups of plants grown in ornamental planting in the Botanical Garden during previous years. For the purpose of making special observations on the conditions involved in the intermittent production of fruit, a crop of 128 plants was grown in 1921. These plants were examined frequently throughout the entire period of bloom, and records were taken for each individual plant as to the character of the flowers opening at a particular time. At the end of the season, observations on the distribution of fruit in regard to the record for the flowers was made. Controlled self- and cross-pollinations were made on many plants.

Every one of the 128 plants produced many pods and the seeds were numerous, but without exception there was decided intermittency in the production of fruit. On several plants there was considerable irregularity in the distribution of pods, but for most plants the pods were in several groups quite as shown in figure 1.

The study of the flowers from day to day together with the results of controlled pollination showed that the intermittent production of fruit is due to repeated cyclic changes in the morphological character of the flowers, which in the course of the cycles give many grades of intersexes. The flowers of any individual plant varied from perfect or fully hermaphroditic flowers to flowers that were functional only as males or only as females, with also innumerable intergrades as to the relative abortion of pistils or stamens. As a rule, however, the loss of sex is decidedly one-sided. When the flowers are hermaphroditic or are female, fruit is produced provided pollination is accomplished; when the flowers are male only, no fruit is produced. The plants pass through alternating periods when the flowers are predominantly hermaphroditic or are female, during which they are productive of fruit, to periods when the flowers are predominantly or only male and fruitless.

The sex character of the flowers, therefore, varies in cycles, which variation makes the intermittent production of fruit a necessary result. The main raceme shown in figure 1 bloomed for a period of 107 days, and on it were produced about 250 flowers. During this time there were for this particular raceme five periods when hermaphroditic and female flowers were produced, with intervening periods when the flowers were staminate only.

In selecting material to illustrate these changes in sex, flowers opening on the same raceme at the same time were taken, the selection being made at a time when the variation was marked. It is, however, seldom that the variation on any one date represents the complete range observed for a plant during a complete cycle. As is shown in the figures, the sex organs
(pistils and stamens) when fully developed are large and conspicuous, and it is easy to observe variations in the degree of their development. The petals were removed from the flowers shown in Plate VI.

The three flowers shown in figure 2, Plate VI, were situated in a raceme in the succession shown and illustrate the range seen for the plant on the particular date when the photo was made; all the flowers were fully and very uniformly male; but the pistils were either normal and functional as in a, decidedly aborted and functionless as in c, or less conspicuously aborted as in b. On the particular date the flowers were varying in respect to femaleness. On other dates, however, maleness was quite as variable.

Maleness is well developed in all the flowers shown in figure 3, although the filaments vary in length and there is one stamen fully aborted in b and one in c. The pistils vary from the highly developed and functional as at a to the extremely aborted as in d. Figure 4 represents flowers of the same plant a few days later, showing extreme abortion in stamens of some flowers and some variation in the size of pistils, although all pistils were functional.

The pistils of the various flowers shown in figure 5 are either well developed (a, b, and c), or decidedly aborted (d, e, and f). The development of stamens is very irregular, and the extremes are seen for a single flower in the various grades as to length of filament and size, development, and dehiscence of anthers. Such irregularities as these are frequently seen, and for numerous plants the condition was more or less present throughout the period of bloom, with, however, no pod production for the flowers that had only aborted pistils.

Figure 6 shows two typical flowers of a plant on a date when the flowers could function only as females.

The four flowers shown in figure 7 show grades of abortion in both pistils and stamens and illustrate very well how the abortion tends to be one-sided, affecting first stamens and then pistils.

The many controlled pollinations that were made revealed that there was in these plants no limitation to fertility through physiological incompatibilities in fertilization. Every plant was highly productive of seed whenever pollen of dehiscing stamens was used on well-developed pistils either in self- or in cross-pollinations. Rudimentary pistils always failed to set seed. Pistils over 2 cm. in length usually produced seed.

Examination of pollen and tests for germination were made of pollen from all sorts of anthers. In large, well-developed anthers, 95% or more of the pollen grains appeared to be normal, and on a sugar-agar medium as many as 80% often germinated, producing tubes as long as 750 μ. In such rudimentary stamens as at d, figure 4, only a few shrunken, empty, partly developed pollen grains were present which did not even swell up when placed in water. In the large-sized but indehiscent anthers of short stamens as in c, figure 4, varying percentages of the pollen appeared to be normal, but in no case did the pollen of such indehiscent anthers germinate when
removed and placed on the same medium which gave good germination for the pollen of normally dehiscing stamens. There were many anthers that were partly dehiscent, that is, they opened to some extent, and the pollen thus shed was often viable in tests and productive of seed in controlled pollinations.

As a rule, the loss of sex for individual flowers was one-sided. When the pistil was rudimentary the stamens tended to be well developed as at c, figure 2. When the stamens were aborted the pistil was usually of good size as at c, figure 4. Occasionally, however, the pistil in flowers with aborted stamens was undersized as at d, figure 4, but cases of complete or extreme abortion of all stamens and of the pistil in the same flower were not observed.

The entire lot of plants were grown throughout under very uniform conditions which favored continued vegetative vigor, and only one generation has been critically studied. Development under conditions which affect differently the vegetative vigor and the length of the growing period may influence and possibly decidedly change the behavior in respect to cyclic changes, quite as such conditions are known to affect the sex of certain plants, particularly of *Arisaema triphyllum* (Pickett, 1915; Schaffner, 1922), from year to year. Definite evidence regarding the direct or indirect influences of environment and the somewhat synchronous changes of sex in the spider flower remains to be obtained.

At the close of the season, when the vigor of plants perceptibly wanes, all parts of the flower, corolla, pistils, and stamens alike, are uniformly undersized. Whether the last flowers that are produced on a plant that reaches old age before being killed by freezing temperatures are as a rule predominantly pistillate or staminate was not determined with certainty. On many such plants the last flowers were decidedly weak in maleness, but for other plants such flowers were decidedly male or bisexual.

**Summary**

In the cultures of *Cleome spinosa* grown for this observational study there was wide variation in the morphological character of the flowers in regard to the relative development of the two kinds of sex organs. The entire range of variations was seen among the flowers of a single plant, giving bisexual flowers, flowers that were functional only as males or as females, and many intergrading types. The variation from one extreme to the other was repeatedly cyclic, which condition results in the intermittent production of fruit.

All of the 128 plants grown under special observation were quite similar; all exhibited the extreme ranges of flower forms or intersexes; in all the production of fruit was more or less intermittent; none was exclusively staminate or pistillate.
Discussion

The alternative loss of maleness and femaleness in the flowers of *Cleome spinosa* and the recurring periodic changes in the sex of the flowers are to be regarded as phenomena of internal and biogenetic regulation closely related to those influences which determine the development of the plant as a whole.

It is, of course, well recognized that in plants as contrasted with animals there is continually the formation of really new organs from a persistent embryonic complex of cells and that this continues until the maturity and death of the plant as a whole. Internal and biogenetic relations of correlation and self-regulation, operating independently or in response to external influences, are hence repeated successively in determining the character of the new organs in the same fashion as they operate once for all in the animal. When there is in addition a long flowering period which overlaps and is coincident with the period of the most vigorous vegetative development, as is the condition in this robust annual *Cleome spinosa*, the conditions are most favorable for a study of the factors influencing the differentiation of sex.

The fact that the loss of sex organs in the flowers of the spider flower is very decidedly one-sided and qualitative is of special significance. When the stamens are aborted the pistil is as a rule functional, and in many cases it is well developed; when the pistil is aborted the stamens are often highly developed and functional. Here, as is the rule in plants, intersexualism does not lead to sterility of the plant or of a flower as a whole. Not a flower was found in which the pistil and all the stamens were extremely aborted, and rather rarely was the abortion of one sex accompanied by the decided abortion of the other sex in the same flower. Abortion of pistils was frequently accompanied by irregular abortion among the various stamens of a flower, but the same irregularity in maleness was also seen for flowers in which there was no abortion of the pistil (see the flowers of fig. 4). While the expression of sex in at least half of the flowers of a plant is decidedly one-sided and alternative, it is not mutually exclusive, for on every plant many bisexual flowers are produced.

It should be noted that the influences operate primarily and almost discriminately on the organs of sex. The pedicels, sepals, and petals are often uniformly well developed for all the types of flowers; but undersized flowers were to be seen (c of fig. 3, and d of fig. 4) in which the flower as a whole is undersized. Such cases, if more general, would suggest a direct relation to waning vigor and decreased food supply such as may be considered to be the direct cause of undersized flowers and of loss of sex in gynomonoecious forms at the end of a period of bloom. That the conditions are more intricate in *Cleome* is evident, for in a marked degree the extreme variations in sex are independent of any other visible change and the various grades of intersexes are present from the beginning of bloom.
Furthermore, the influences that affect the sex of a single flower often extend to groups of flowers. Thus there is a period of maleness, which is followed by a period of femaleness or of bisexualism, and this in turn is followed by maleness. Flowers in the same condition as to sex are grouped along the raceme. There is a series of cyclic changes all occurring during the period of continuous bloom.

These qualitative changes in sex in flowers of *Cleome spinosa* do not involve the transformation of organs of one sex into organs of the other sex after differentiation has begun, as is the case in many of the intersexes reported in animals (Goldschmidt and Poppelbaum, 1914; Goldschmidt, 1916; Banta, 1916; Lillie, 1917; Sexton and Huxley, 1921). Here the change is accomplished, as it is in dioecious plants, by the abortion of one or the other kind of sex organs. The relative position of each in the flower as a whole is maintained, but the differentiation giving male and female flowers (along with bisexual flowers) is as complete as is seen in many species of dioecious plants. The differential determination of sex in repeated cyclic alternative changes as they occur in *Cleome spinosa* shows to what degree the internal correlative differentiations in development may be extended to the organs of sex after the plant as a whole has passed from the exclusively vegetative to the reproductive stage. At the time of the transition to the reproductive stage, the change is not necessarily complete and discontinuous, nor are the flowers produced in succession necessarily of the same grades of sex. Even when the flowers appear to be morphologically the same there may be a decided cyclic change in their physiological character, as is the case with *Brassica chinensis* and *B. pekinensis* (Stout, 1922). The contrast between these species of *Brassica* and *Cleome spinosa* illustrates well the different types of sterility that may develop in plants and the different expressions of cyclic regulation of them. In these Brasicas there is frequently rather decided abortion of flowers at the time of transition from vegetative to reproductive organs; in Cleome no indication of such abortion is present, the first flowers to appear being often fully developed as hermaphrodites. In the Brasicas there is a somewhat extended period of flower formation with flowers all morphologically bisexual—but in which the physiological relations in fertilization may vary in a very definite and single cycle; in *Cleome spinosa* there is no variation in the physiological nature of stamens and pistils that are at all functional in so far as these may be tested by the relations of fertilization, but there is the cyclic alternation in the morphological development of the organs of sex. This comparison illustrates two rather widely different expressions of sex in its relation to fertility and sterility.

The conditions in *Cleome spinosa* favor the view that, as held by Yam-polsky (1920), there is a general tendency away from hermaphroditism toward dioecism among the higher plants. In the persistence of perfect flowers in greater or less numbers along with those which are more or less
purely staminate or pistillate, *Cleome spinosa* is like most species which are in the transition stages toward dioecism. The alternate appearance of male, female, and hermaphroditic flowers in a raceme of course favors crossing, and when this alternation tends to be synchronous on all the branches of a plant, selfing is largely prevented except in the case of the hermaphroditic flowers.

In the spider flower, with its long flowering period and its alternation of maleness and femaleness in the racemes, it is evident that practically the whole vegetative feeding power of every plant is drawn upon for seed production. The conditions are markedly different, and we may consider them more highly adaptive to the demands of reproduction, than is the case in strictly dioecious plants in which seed production is confined to one of each pair of male and female plants. We may, perhaps, characterize the sex conditions in *Cleome spinosa* as effecting a sort of *super-dioecism* in that the conditions favor both reproduction and crossing for each individual.

Certain points regarding the determination of sex in the flowers of *Cleome spinosa* are clear. The conditions illustrate well the fact that the morphological differentiations of sex are fundamentally an extension of the phenomena of somatic differentiations. The expressions of differential qualities in leaves, stems, and flowers, with further differentiation of calyx, corolla, pistil, and stamens, with still further differentiations of tissue within each, are all recognized as one-sided, qualitative, and alternative expressions in protoplasmic units that are alike and which still remain alike in fundamental constitution. Even the physically qualitative division of germ plasm in the reduction divisions is found in regeneration experiments and in parthenogenesis not to be a direct and absolute condition in the alternation of generations. The theory of sex chromosomes decidedly fails in general application to plants, and even in animals, where its application seems most marked, sex is often intergrading and reversible, showing that there is alternative expression rather than alternative inheritance.

In *Cleome spinosa* it is evident that there are rather special and perhaps very specific stimulating and inhibiting influences which regulate the development of the sex organs. Whether these influences are substantive or more of the nature of stimuli, their action is cyclic and decidedly alternative. The results clearly show that sex of flowers is determined progressively as they are formed in response to regulation by internal biogenetic conditions.

**NEW YORK BOTANICAL GARDEN**

**LITERATURE CITED**


EXPLANATION OF PLATE VI

Each group of flowers is from the same raceme on the same date. Petals have been removed. The scale in inches shows the reduction from natural size.

Fig. 2. Three sister flowers uniform as to maleness but highly variable in femaleness.

Fig. 3. The stamens of the four flowers vary as to length; one stamen in b and one in c are aborted; all others are highly functional. Pistils are functional in a, b, and c, but aborted in d.

Fig. 4. Four flowers from same plant as those of figure 3, several days later. Pistils vary as to length but all are functional. Stamens all excellent in a, two much aborted and indehiscent in b, all indehiscent in c, and all much aborted and containing no pollen in d.

Fig. 5. Pistils variable; in a, b, and c, fully functional; in d, e, and f, rather aborted. Stamens highly variable in each flower irrespective of the condition of the pistil.

Fig. 6. All stamens much aborted or rudimentary. Pistils somewhat undersized but functional.

Fig. 7. Abortion of stamens only, as at a, or of pistil, as at c and d, with a flower (b) fully hermaphroditic; all in bloom at the same time on the same raceme. Illustrates well the marked one-sided abortion of sex organs.
Stout: Alternation of Sexes

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