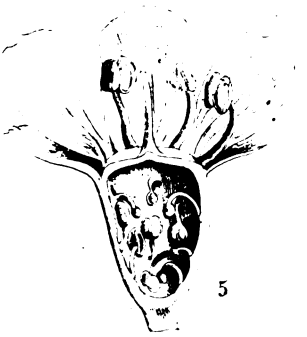
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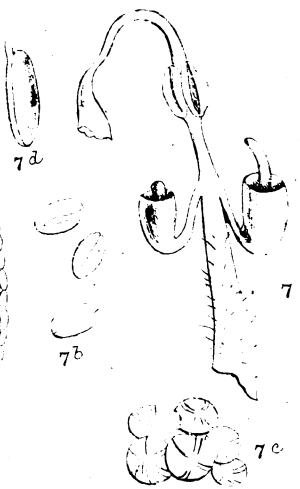
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SEXUALITY IN PLANTS.

By MAXWELL T. MASTERS, M.D., F.R.S.

[PLATE CIII.]

IT has long since become unnecessary to offer any argument or illustration in support of the doctrine of sexuality in plants. Among the so-called flowerless plants even, the evidence of the existence of distinct sexes is now so overwhelming that there are few who hesitate to believe in its occurrence, even in those cases where only one of the two sexes has up to this time been demonstrated. Linnæus, to whom, most of all, we owe the promulgation of the doctrine, though he was by no means the first to propound it, proceeded to establish it by inductive, circumstantial evidence. He brought forward comparatively little in the way of direct proof or absolute demonstration, even among flowering plants, while the actual existence of sexes in the so-called flowerless plants has been questioned up to within quite recent times. It is a singular fact, however, that the whole process of fertilisation has been, generally speaking, more thoroughly and completely demonstrated among the so-called Cryptograms, long considered as a sexual, than among the more highly developed flowering plants. It is curious also to remark the different views now taken as to the process from those which were held originally. As soon as it was clearly perceived that the stamens and the pistils, or their contents, were the essential agents in the process of fertilisation, it was naturally surmised that the pistil of every given flower was fertilised by the pollen of the same flower. Under this supposition many curious contrivances which were observed were at once set down as so many aids and promoters of self-fertilisation.

Sprengel was one of the first to show the fallacies of these observations, and to demonstrate the frequent existence of cross-fertilisation, whether effected by the agency of winds or by pollen-carrying insects.

Vaucher added other illustrations, but it was not till the publication and experimental researches of Darwin that the subject received the attention it merited. Darwin's classical paper on *Primula*, in the "Journal of the Linnean Society," followed up by similar memoirs on *Lythrum*, *Linum*, &c., stirred up a host of observers. Large numbers of new facts were recorded, all confirming the idea that while self-fertilisation is not impossible, and is indeed in some few cases inevitable, yet in the majority of instances some provision for cross-fertilisation is afforded, if not constantly, at least occasionally. Hildebrand, Delpino, Alfred Bennett, and others, have correlated these facts, and, making allowance for exceptional instances, they one and all confirm the views expressed by Darwin. The observations and experiments of these gentlemen are so well known, and the records of them are so accessible, that we do not propose now to occupy space by making further allusions to them. Suffice it merely to say, that these observations have reference to the facilities offered by various structural modifications for favouring cross-fertilisation and preventing self impregnation or *vice versâ*, and they all tend to show the advantage that accrues from an occasional cross.

Our object in the present communication has reference to another department of the subject; and it is one we think it desirable to call attention to, as it appears not to receive so much attention as its importance demands. We allude particularly to the circumstances promoting the development of pollen-forming or ovule-bearing flowers respectively.

Before proceeding further we ought to explain that in using the expressions male, female, or hermaphrodite flowers, we do so, unless otherwise stated, with reference to structural conditions rather than to physiological office. The term "bisexual" is preferable to that of hermaphrodite, as not implying any physiological distinction.

For our present purpose, then, a flower with stamens and pistils perfectly formed is bisexual or hermaphrodite, even though its pistil be not fertilised by its own pollen, but by that derived from some other source.

For convenience sake, we take a bisexual flower as our starting-point; and we propose to allude to various not infrequent changes observed in flowers of that description, in consequence of which their sexual organisation becomes more or less materially modified.

A plant usually producing flowers, bisexual or hermaphrodite as to structure, may bear flowers of one sex only by the simple arrest of growth. Thus, if the stamens of any given flower be arrested in their development, the blossom becomes

female, as happens not unfrequently in some buttercups, lesser celandine (*Ranunculus*), and others.

Conversely, if the pistil be not developed the adult flower will be male, as happens in many Umbellifers and Caroyphylleæ.

The exact opposite of this change occurs when flowers usually of one sex become bisexual by the development of stamens or of pistils, as the case may be. Instances of this kind are common in almost all normally unisexual flowers. If the unisexual condition of an ordinary bisexual plant be considered from a structural point of view as an arrest of development, the present instance must be attributed to an exaltation of that process.

There is another way in which an ordinarily one-sexed flower may become two-sexed, and that is by the more or less perfect change of stamens into pistils, or of pistils into stamens. This is sometimes the result of a substitution of one part for another, but in other cases of an actual permutation. A stamen becomes converted at a certain stage of its growth into a pistil, or *vice versâ*. Such changes are by no means uncommon in plants. We may thus have a stamen assuming the guise of a pistil, a pistil endowed with all the attributes of a stamen; we may even have pollen formed within the tissues of the ovule itself, as has been seen in a passion-flower and in a rose. A more complete hermaphroditism can hardly be conceived.

So far we have been dealing with individual flowers, but analogous changes occur throughout the whole organism. Thus many plants, under ordinary circumstances, produce unisexual flowers, male and female, on the same individual. Such are the plants called *monœcious*. Now it sometimes happens that plants of this character become entirely unisexual by the development of male or of female flowers, only to the exclusion of the other. Such occurrences are not uncommon in mulberries and walnuts.

The converse of this is, when a plant ordinarily producing flowers of different sexes on different individuals (*diœcious*) forms flowers of both sexes on the same plant, becomes, in other words, monœcious. This occurs occasionally in the hop.

These changes in the structural condition of the flower, variously modified and combined in different cases, constitute all the changes in the sexual organisation of the flower which concern us at present. May we not say of these puzzling transformations what Horace said of a girlish-looking youth—

> Mire sagaces falleret hospites
> Discrimen obscurum, solutis
> Crinibus ambiguoque vultu.

It is obvious that the accurate determination of the causes of the changes above alluded to is a point not only of high physiological interest, but also of much practical value. A working gardener is often puzzled, and his employer disgusted, at finding his strawberries barren, his vines refusing to set, his melons 'shy-bearers.' Where seed is wanted, and little, and that perhaps of bad germinating power, is produced, the disappointment is naturally great. We are far from saying that the reasons for these untoward events can, in the present state of our knowledge, be at all times determined; but we do say that the cause is often obvious, and that few more striking instances of the benefit which science may confer on practice can be adduced than those which vegetable physiology has conferred on the cultivator.

We have seen that the structural changes affecting the reproductive organs of the flower may be reduced to—1, an arrest; and 2, to exaltation; or 3, to perversion of growth or of development. In seeking the causes of these changes it would seem, at first sight, natural to refer an arrested growth to a relatively deficient supply of nutriment, or to some other debilitating or obstructing cause. The opposite condition might as readily be accounted for by an increased food supply, or by the presence of other favourable conditions. No doubt this is true so far as it goes, but the problem is more complex than it appears to be on the surface. An arrest of growth, for instance, may arise from a superabundance of food, or from an inability to assimilate it. One may starve in the midst of plenty. Again, it is notorious that exaltation of development, in one organ or set of organs, may be a sequela of impaired nutrition; in others, the principle of compensation comes into play in such cases—if one part is debilitated, another takes on proportionately more vigorous development. If the balance be once disturbed, the opportunity for change is at once, and of necessity, afforded. To further illustrate this matter, we may now advert to the theory of Dr. R. Spruce; and which, if not proved, at least affords a valuable focus for the concentration and correlation of evidence, and a good stand-point from which to discuss it. According to this theory the progenitor of existing plants had structurally and functionally hermaphrodite flowers. In course of time the economy of force accruing from division of labour led, and still leads, to a separation of the sexes. The health and vigour of the individual plant would be promoted by the separation, the number and vigour of its offspring increased. Once the equilibrium disturbed, natural selection would tend to perpetuate the change as one generally advantageous to the plant. The changes in question do not amount to the actual

annihilation or obliteration of either sex. In a unisexual flower one sex, though not actually, may be at least potentially present—nay, must be, if Darwin's theory of pangenesis be true—and so it happens that, when any change of conditions occurs, the heretofore latent gemmules start into life, and the unisexual is once more replaced by the bisexual state. In other words, a reversion occurs to the assumed primitive condition.

There are numerous instances among one-sexed plants to prove that the missing organs are latent, rather than altogether deficient. It has already been stated that many one-sexed flowers are so by arrest of development; the male or the female element, as the case may be, is present, but in a latent or rudimentary state. So many flowers which in the adult state are one-sexed, are in the young state structurally hermaphrodite. Indian corn or maize, the two sexes of which are very distinct in the fully developed condition, is said to have primordially bisexual flowers. A plant which in one year, or it may be for a succession of years, produces flowers of one sex only, may in another season form either bisexual blossoms, or flowers of both sexes on the same plant. We have seen cases of the first kind in the ash and in some of the maples; of the second in walnuts, mulberries, and hops; while in certain kinds of vines, and in some strawberries, the fact alluded to is notorious. Dr. Spruce ("Journ. Linn. Soc." xi. 1871, p. 95) records cases of the same kind in palms growing about the Amazon, and in which the trees produce chiefly female flowers one year, and take a comparative rest in the following one by forming male flowers, whose formation does not so greatly tax the energies of the tree. Evidences of the same tendency are afforded by the circumstances that the seeds of unisexual plants produce seedlings, now of one, now of another, sometimes of both sexes, in very unequal proportions. The seeds of a Papaw, *Carica Papaya*, which were collected from a female plant in South America, produced, when sown at Mentone, seedlings which developed male flowers, and afterwards bisexual flowers mixed with the males—a condition never observed by the person who furnished the seed, though his attention was specially called to it. It seems probable that the changed conditions of growth may have induced the alteration; but, as we shall see presently, such an assumption must not be accepted without question, as other causes may produce like results. Cuttings, also, and buds taken from a plant of one sex, though they will in general perpetuate the characters of that sex, have been occasionally known to develop flowers of the opposite sex.

Dr. Spruce has not, so far as we know, done more than make very brief reference to his theory, and has not yet sought to

establish it in detail.* We therefore run some risk of misinterpreting his views, but we would suggest that if it be asserted that the progenitors of our existing flowers were hermaphrodite, and that they have since become unisexual, then the numerical proportion of fossil plants with hermaphrodite flowers ought to be very much larger than it is. Again, we ought to find in the older strata, as compared with more recent deposits, a much larger proportion of hermaphrodite than of one-sexed flowers, whereas the exact reverse holds good. We are quite aware that too much stress must not be laid on any conclusion derived from what remain to us of fossil plants.

There is now-a-days, and probably always was, a much larger proportion of woody plants with one-sexed flowers, and the latter would stand a better chance of being preserved than would the softer-tissued more ephemeral-lived plants. Lecoq estimates the proportion of unisexual species in central France among woody plants or perennials at one in eight, while in annuals the proportion is one in thirty-five. With hermaphrodite flowers, again, the frequent aggregation of one-sexed flowers into dense masses or catkins would necessarily impart a degree of permanence to them not possessed by plants producing their flowers in smaller numbers, or in less compact masses. Still, even if the necessary allowances be made, we do not think Dr. Spruce's views receive support from geology. To us it appears that the bulk of evidence goes to show that annual plants, or those which flower once only in the course of their lives, are of more recent origin than woody plants which flower repeatedly, while the proportion of one-sexed flowers among annuals is much less than in the case of longer-lived plants.

There is another point of view from which this question may be approached, and that may perhaps be more consonant with Dr. Spruce's real view than that which we have attributed to him, and that is the primordial oneness of sex. We are so much in the habit of dwelling on the differences of sex, that we are apt to overlook the fact that those differences do not exist in the first instance, and that even in the adult state they are characteristic of the individual, not of the species. In the life of all creatures there is a period when there is no perceptible difference of sex, and it seems to depend on circumstances which sex shall ultimately be developed. Now, if there were any intrinsic difference such as by our everyday language we imply that there is, it would surely be manifest from the beginning, and not be a subsequent evolution.

* Dr. Spruce's papers on this subject may be found in the "Gardener's Chronicle," 1870, p. 826, and in the "Journal of the Linnean Society," 1871, vol ix. p. 96.

We take it, then, that there is a primordial oneness of sex, as Plato long since argued, and in that sense we agree with Dr. Spruce. We are constantly meeting in plants with traces of this essential unity of sex. We can see it in the development of all flowers; we meet with it frequently in the structural changes from one sex to the other, and to which we have already drawn attention. If we find the same organ bearing, at the same time, on one side pollen and on the other side ovules—a by no means unusual occurrence—it is difficult to conceive that there can be so great an intrinsic difference between the sexes as is usually admitted. If we find the pistil producing pollen, and the stamens forming ovules—as happens not unfrequently in the common stonecrop and in the wallflower—our belief in the absolute diversity of the two sexes becomes less implicit. If we meet with ovules bearing pollen in their interior, as has now been seen in species of passion-flower by Mr. J. A. Salter, and by the writer in a rose, our faith in the duality of sex becomes well nigh uprooted. In face of such evidence is it not reasonable to suppose that as sexual characteristics of any kind are themselves secondary in point of development, and individual, not specific, so the dual nature of the sexual principle, so conspicuous in the adult organism, is a later development or evolution from an originally homogeneous unity? The old tradition of the development of Eve from the rib of our forefather Adam may not after all be so purely mythical an assertion. What Milton said of the spirits may, if we exclude the notion of volition, be properly applied to plants:—

> "Spirits, when they please,
> Can either sex assume, or both."

It remains now to enquire what are the causes which disturb the equilibrium in the first instance, and to ascertain what are the special circumstances which favour the development of one sex at the expense of the other.

With reference to the first point, it would appear that although very slight causes are sometimes sufficient to deflect the balance, yet at others, and those more frequent, much more violent changes are powerless to bring about such a result.

Allusion has been already made to a seedling Papaw, the produce of American seed developing hermaphrodite flowers when grown on the shores of the Mediterranean, and the changed conditions have been assumed to be sufficient to account for the phenomenon. On the other hand we have seen a male plant of the Papaw, cultivated for years in the Oxford Botanic Garden, suddenly produce bisexual flowers without obvious change of condition; and numerous parallel changes are familiar to all observers. Sometimes in these cases

it is not made sufficiently clear whether ripe fruit only, or ripe fruit containing ripe seeds capable of germinating, are developed—a very important element to be considered, as the fruit may often ripen and develop only imperfect seed or none at all.

The structural changes hitherto effected as a consequence of man's interference, either intentionally or of necessity, are relatively slight. Consider, for instance, the artificial conditions under which plants are transplanted, pruned, grown, fed in gardens, and then contrast the rare instances in which any absolute or essential changes in structure (not merely of degree of development, more or less) occur. Important structural changes of a relatively permanent character appear, as a rule, to be brought about very slowly and gradually.

As regards functional activity, however, the case is very different. Very slight alterations will often immediately and profoundly modify the fertility of a given flower and the vigour of its seedlings. Cases are recorded wherein a flower ordinarily sterile, when fertilised by its own pollen, has developed perfect fruit and seeds when grafted on to some other species. Cultivation, climatic changes, diseases, injuries, all have a tendency to influence for good or ill the reproductive functions of plants, even though the change in circumstances be apparently slight, and the structural alteration consequent on them absolutely inappreciable.

We have already cited instances where altered climatal conditions, as the transfer of a plant from Europe to America, have, on the other hand, induced changes in the sexual organisation of the plant. There are several cases cited where a species growing within certain latitudes is of one sex chiefly, while the same species growing in other latitudes developes mainly flowers of the opposite sex. Instances of a similar character are related in reference to moisture. A willow growing in a very wet locality has been known to produce female flowers only, while in a dry place male catkins only were produced. In the case of some Begonias, which, under ordinary circumstances, produce separate male and female flowers on the same plant, Mr. Anderson Henry has succeeded in inducing the formation of female flowers only by removing two out of the three stigmatic lobes, and fertilising the remaining one. All the plants, four or five in number, which have resulted from this cross, have produced female flowers only. Mr. Henry has repeated the experiment with the same result. Such observations as these need confirmation and extension; and from the ease with which they may be made, and their importance, may be commended to the special notice of amateurs. It is obvious also that in the case of ordinarily

hermaphrodite flowers the time at which an alteration of the "environment" occurs must be taken into consideration. As a rule, the stamens are developed before the pistil; hence if some check to growth accrue, it may occur before the formation of the pistil, when a staminiferous flower would result. Or, again, the circumstances inducing an arrest of growth at the period when the stamens are forming may subsequently change, and the pistil be regularly formed, though the stamens remain undeveloped or abortive.

That the precise period at which growth and development take place is an element of great importance in such matters, is one which no physiologist is likely to dispute. Not to mention cases in the animal kingdom, it is sufficient to say that the conformation of flowers produced out of their accustomed season is very often more or less deranged; their position is often different, their form changed, the number and arrangement of their parts altered. Of course the reproductive organs undergo corresponding changes. The flowers of apples or pears which are occasionally produced on the so-called "midsummer shoots" have perfect stamens, but rarely perfect pistils. Under ordinary circumstances, the flowers we have mentioned are developed in autumn, on short stunted branches or spurs, and remain quiescent till the following spring; but in the cases under consideration an imperfect flower is formed within a few weeks, at the end of a long, weakly shoot, also of rapid growth. There is nothing surprising in this; it is just what might be expected, and it furnishes an illustration of our argument that the period at which certain changes occur is an element of cardinal importance in the determination of the nature of those changes. Baillon records having met with an hermaphrodite flower in June on the common hazel. It would be sufficiently extraordinary to meet with such a flower at any time, but it seems more consistent to meet with such a flower in summer rather than in winter, the normal period of flowering.

The bearing that this part of our subject has on practical gardening is obvious, and particularly in the case of forcing. Practical gardeners know well that in forcing vines, pines, strawberries, cherries, cucumbers, or indeed any plant which is required to produce its flowers and fruit out of due season, they cannot be too careful in the timely regulation and adjustment of the heat and moisture at their disposal. Want of care, or deficient judgment, will defeat the object aimed at, and a crop of leaves only, or sterile "blind" flowers, or flowers which refuse to "set," will be the consequence. The anatomist knows the structural reasons for this; the physiologist speculates on the causes which put the structures into action; the practical man, taught by experience, knows how to avail himself both of the one and

the other—if not to make the machine, at least to set it going, and regulate its action according to his wishes.

In this place we may appropriately call attention to the opinions of Mr. Meehan on the sexuality of plants, and which demand attention as the opinions of a practised cultivator, a good observer, and a shrewd reasoner.* As the result of his observations, he comes to the conclusion that in plants a high degree of vigour produces the female sex, while a less robust constitution is sufficient for the development of the pollen. In this manner the alternation sometimes observed in unisexual plants may be accounted for. A plant producing fruit, and more particularly ripe seed, for a succession of years, becomes more or less exhausted, and during the period when it is recruiting its energies it forms male flowers only. Mr. Meehan bases his theory on the relative position of the flowers of the two sexes, showing that the female flowers are, as a rule, placed on the strongest axial parts, the male ones on the weakest. As a consequence of this, the female flowers are so placed as to receive the direct flow of the nutrient fluid, while the male flowers often derive their supplies from collateral, or less direct sources, and in smaller quantities. He further goes on to show that the invigorating effects of climate, of manuring, &c., tend more particularly to the development of the female rather than to that of the male flower.

Apart from ascertained facts, it seems reasonable to suppose that a less degree of vital energy would be required for the staminate flowers, whose functions are much sooner fulfilled, than for the pistillate flowers, whose office of forming, protecting, ripening the pistil, and more especially its contents (the ripe seed), naturally occupies so much longer a period, and involves so much larger a demand on the resources of the plant. There are several facts which lend colour to this theory. In America, strawberry-blossoms are frequently unisexual. In this country, also, some varieties are apt to produce "blind," i.e. sterile flowers. The same thing happens in vines, and indeed in many other plants. Spruce and Meehan, as we have seen, would consider this tendency to produce unisexual flowers as an evidence of progress; and so indeed it may be, on the principle of division of labour. The gardener, however, looks upon the occurrence in quite a different light, and does his best to rid himself of such undesirable plants. But if the advantage accruing from division of labour, and specially from the operation of cross fertilisation, were fully recognised by him, he should rather promote than discourage such a tendency, and counteract the sterility by the artificial employment of pollen from some

* Cited in "Gardener's Chronicle," 1870, p. 243.

other plant or variety. In this manner, too, he would counteract that weakness of constitution, the result of continual in-and-in breeding, and which is so apparent in many of the higher bred flowers and vegetables of the present day, and which leaves them an easy prey to disease and parasitic fungi. At any rate, we owe to the observation of practical gardeners the establishment of the fact that a relatively high temperature is most conducive to the formation of stamens in the case of strawberries, a low temperature to that of pistils. So again, in the case of vines, it has been observed that a high temperature conduces specially to the formation of tendrils, a low one to that of fertile flowers. It is probable, however, that varying conditions of moisture may have as much effect in this way as the mere variation of temperature.

That parasitic fungi should determine the formation of stamens seems at first sight sufficiently remarkable. Nevertheless such is the opinion held by M. Cornu, in France, and it was independently brought before the notice of the British Association at Exeter, by Miss Becker. Moreover, the notion receives the assent of the veteran mycologist, the Rev. M. J. Berkeley, than whom none more competent to express an opinion on such a subject. The facts are as follows:—The common *Lychnis* of our hedges, *Lychnis diurna*, has unisexual and dicœcious flowers; but when affected by a parasitic fungus, the flowers, which should be pistillate only, develop stamens also. This is attributed by Miss Becker to the fact that the fungus (*Ustilago antherarum*), although able to penetrate the plant, can only fructify in the anthers, and consequently it becomes the determining cause of the production of the stamens in the normally female flower. We have not all the evidence before us, on which account we find it difficult to understand how the presence of the fungus in the anthers should be taken as a proof that they (the anthers) were called into development by the fungus. That other flowers on the same plant unaffected with fungus should have pistils only and no stamens, is surely not to be taken as a proof that parasitic fungi can cause the development of stamens. The origin of sexual differences, and the power of inducing in animals the appearance of one or other at will, have from the oldest times exercised the thoughts of philosophers. As we have seen, the solution of the problem is not only of the highest interest as a matter of science, but also as regards the direct material welfare of mankind. Without intending any disparagement to the devotees of the sister science of zoology, we may yet affirm confidently that the botanists and gardeners between them have so far advanced considerably beyond their *confrères* in the unravelling of this, by no means the least, of the mysteries of life.

EXPLANATION OF PLATE CIII.

FIG. 1. Flower of willow, bearing one stamen, and one pistil. (Mag.)
„ 2. Normal male flower of the same species. (Mag.)
„ 3. Capsule of poppy, surrounded by secondary capsules, resulting from the substitution of pistils for stamens. (Nat. Size.)
„ 4. Stamens of gourd, bearing ovules (after Berkeley). (Nat. Size.)
„ 5. Pistil of Bæckea, bearing stamens in the interior in place of ovules. (Mag.)
„ 6. Scale from double hyacinth, bearing an anther above, and two ovules beneath. (Mag.)
„ 7. Filament of a rose, bearing below two imperfect polliniferous ovules, and two-celled anther, and terminating in a dilated stigma. (Mag.)
„ 7A. Ovule from the above, compressed, and showing the partial conversion of its tissues to those of an anther. (Mag.)
„ 7B. Pollen-cells from ovule. (Mag.)
„ 7C. Spiral anther-cells from ovule. (Mag.)
„ 7D. Normal ovule of rose.
„ 8. Hop, bearing male and female flowers on the same inflorescence.