THE

EFFECTS

OF

CROSS AND SELF-FERTILISATION.

CHAPTER I.

INTRODUCTORY REMARKS.

Various means which favour or determine the cross-fertilisation of plants—Benefits derived from cross-fertilisation—Self-fertilisation favourable to the propagation of the species—Brief history of the subject—Object of the experiments, and the manner in which they were tried—Statistical value of the measurements—The experiments carried on during several successive generations—Nature of the relationship of the plants in the later generations—Uniformity of the conditions to which the plants were subjected—Some apparent and some real causes of error—Amount of pollen employed—Arrangement of the work—Importance of the conclusions.

THERE is weighty and abundant evidence that the flowers of most kinds of plants are constructed so as to be occasionally or habitually cross-fertilised by pollen from another flower, produced either by the same plant, or generally, as we shall hereafter see reason to believe, by a distinct plant. Cross-fertilisation is sometimes ensured by the sexes being separated, and in a large number of cases by the pollen and stigma of the same flower being matured at different times. Such plants are called dichogamous, and have been divided into two sub-classes: proterandrous species, in which the pollen is mature before the stigma, and proterogynous species, in which the reverse occurs; this latter form of dichogamy not being nearly so common as the other. Cross-fertilisation is also ensured, in many cases, by mechanical contrivances of wonderful beauty, preventing the impregnation of the flowers by their own pollen. There is a small class of plants, which I have called dimorphic and trimorphic, but to which Hildebrand has given the more appropriate name of heterostyled; this class consists of plants presenting two or three distinct forms, adapted for reciprocal fertilisation, so that, like plants with separate sexes, they can hardly fail to be intercrossed in each generation. The male and female organs of some flowers are irritable, and the insects which touch them get dusted with pollen, which is thus transported to other flowers. Again, there is a class, in which the ovules absolutely refuse to be fertilised by pollen from the same plant, but can be fertilised by pollen from any other individual of the same species. There are also very many species which are partially sterile with their own pollen. Lastly, there is a large class in which the flowers present no apparent obstacle of any kind to self-fertilisation, nevertheless these plants are frequently intercrossed, owing to the prepotency of pollen from another individual or variety over the plant's own pollen.

As plants are adapted by such diversified and effective means for cross-fertilisation, it might have been inferred from this fact alone that they derived some great advantage from the process; and it is the object of the present work to show the nature and importance of the benefits thus derived. There are, however, some exceptions to the rule of plants being constructed so as to allow of or to favour cross-fertilisation, for some few plants seem to be invariably self-fertilised; yet even these retain traces of having been formerly adapted for cross-fertilisation. These exceptions need not make us doubt the truth of the above rule, any more than the existence of some few plants which produce flowers, and yet never set seed, should make us doubt that flowers are adapted for the production of seed and the propagation of the species.

We should always keep in mind the obvious fact that the production of seed is the chief end of the act of fertilisation; and that this end can be gained by hermaphrodite plants with incomparably greater certainty by self-fertilisation, than by the union of the sexual elements belonging to two distinct flowers or plants. Yet it is as unmistakably plain that innumerable flowers are adapted for cross-fertilisation, as that the teeth and talons of a carnivorous animal are adapted for catching prey; or that the plumes, wings, and hooks of a seed are adapted for its dissemination. Flowers, therefore, are constructed so as to gain two objects which are, to a certain extent, antagonistic, and this explains many apparent anomalies in their structure. The close proximity of the anthers to the stigma in a multitude of species favours, and often leads, to self-fertilisation; but this end could have been gained far more safely if the flowers had been completely closed, for then the pollen would not have been injured by the rain or devoured by insects, as often happens. Moreover, in this case, a very small quantity of pollen would have been sufficient for fertilisation, instead of millions of grains being produced. But the openness of the flower and the production of a great and apparently wasteful amount of pollen are necessary for cross-fertilisation. These remarks are well illustrated by the plants called cleistogene, which bear on the same stock two kinds of flowers. The flowers of the one kind are minute and completely closed, so that they cannot possibly be crossed; but they are abundantly fertile, although producing an extremely small quantity of pollen. The flowers of the other kind produce much pollen and are open; and these can be, and often are, cross-fertilised. Hermann Müller has also made the remarkable discovery that there are some plants which exist under two forms; that is, produce on distinct stocks two kinds of hermaphrodite flowers. The one form bears small flowers constructed for self-fertilisation; whilst the other bears larger and much more conspicuous flowers plainly constructed for cross-fertilisation by the aid of insects; and without their aid these produce no seed.

The adaptation of flowers for cross-fertilisation is a subject which has interested me for the last thirty-seven years, and I have collected a large mass of observations, but these are now rendered superfluous by the many excellent works which have been lately published. In the year 1857 I wrote * a short paper on the fertilisation of the kidney bean; and in 1862 my work 'On the Contrivances by which British and Foreign Orchids are Fertilised by Insects' appeared. It seemed to me a better plan to work out one group of plants as carefully as I could, rather than to publish many miscellaneous and imperfect observations. My present work is the complement of that on Orchids, in which it was shown how admirably these plants are constructed so as to permit of, or to favour, or to necessitate cross-fertilisation. The adaptations

* 'Gardeners' Chronicle,' 1857, p. 725, and 1858, pp. 824 and 844. 'Annals and Mag. of Nat. Hist. 3rd series, vol. ii. 1858, p. 462.

for cross-fertilisation are perhaps more obvious in the Orchideæ than in any other group of plants, but it is an error to speak of them, as some authors have done, as an exceptional case. The lever-like action of the stamens of Salvia (described by Hildebrand, Dr. W. Ogle, and others), by which the anthers are depressed and rubbed on the backs of bees, shows as perfect a structure as can be found in any orchid. Papilionaceous flowers, as described by various authors—for instance, by Mr. T. H. Farrer—offer innumerable curious adaptations for cross-fertilisation. The case of *Posoqueria fragrans* (one of the Rubiaceæ), is as wonderful as that of the most wonderful orchid. The stamens, according to Fritz Müller,* are irritable, so that as soon as a moth visits a flower, the anthers explode and cover the insect with pollen; one of the filaments which is broader than the others then moves and closes the flower for about twelve hours, after which time it resumes its original position. Thus the stigma cannot be fertilised by pollen from the same flower, but only by that brought by a moth from some other flower. Endless other beautiful contrivances for this same purpose could be specified.

Long before I had attended to the fertilisation of flowers, a remarkable book appeared in 1793 in Germany, 'Das Entdeckte Geheimniss der Natur,' by C. K. Sprengel, in which he clearly proved by innumerable observations, how essential a part insects play in the fertilisation of many plants. But he was in advance of his age, and his discoveries were for a long time neglected. Since the appearance of my book on Orchids, many excellent works on the fertilisation of flowers, such as those by Hildebrand, Delpino, Axell,

* 'Botanische Zeitung,' 1866, p. 129.

and Hermann Müller,* and numerous shorter papers, have been published. A list would occupy several pages, and this is not the proper place to give their titles, as we are not here concerned with the means, but with the results of cross-fertilisation. No one who feels interest in the mechanism by which nature effects her ends, can read these books and memoirs without the most lively interest.

From my own observations on plants, guided to a certain extent by the experience of the breeders of animals, I became convinced many years ago that it is a general law of nature that flowers are adapted to be crossed, at least occasionally, by pollen from a distinct plant. Sprengel at times foresaw this law, but only partially, for it does not appear that he was aware that there was any difference in power between pollen from the same plant and from a distinct plant. In the introduction to his book (p. 4) he says, as the sexes are separated in so many flowers, and as so many other flowers are dichogamous, "it appears that nature has not willed that any one flower should be fertilised by its own pollen." Nevertheless, he was far from keeping this conclusion always before his mind, or he did not

* Sir John Lubbock has given an interesting summary of the whole subject in his 'British Wild Flowers considered in relation to Insects,' 1875. Hermann Müller's work 'Die Befruchtung der Blumen durch Insekten,' 1873, contains an immense number of original observations and generalisations. It is, moreover, invaluable as a repertory with references to almost everything which has been published on the subject. His work differs from that of all others in specifying what kinds of insects, as far as known, visit the flowers of each species. He likewise enters on new ground, by showing not only that flowers are adapted for their own good to the visits of certain insects; but that the insects themselves are excellently adapted for procuring nectar or pollen from certain flowers. The value of H. Müller's work can hardly be over-estimated, and it is much to be desired that it should be translated into English. Severin Axell's work is written in Swedish, so that I have not been able to read it.

see its full importance, as may be perceived by anyone who will read his observations carefully; and he consequently mistook the meaning of various structures. But his discoveries are so numerous and his work so excellent, that he can well afford to bear a small amount of blame. A most capable judge, H. Müller, likewise says:* "It is remarkable in how very many cases Sprengel rightly perceived that pollen is necessarily transported to the stigmas of other flowers of the same species by the insects which visit them, and yet did not imagine that this transportation was of any service to the plants themselves."

Andrew Knight saw the truth much more clearly, for he remarks,† "Nature intended that a sexual intercourse should take place between neighbouring plants of the same species." After alluding to the various means by which pollen is transported from flower to flower, as far as was then imperfectly known, he adds, "Nature has something more in view than that its own proper males should fecundate each blossom." In 1811 Kölreuter plainly hinted at the same law, as did afterwards another famous hybridiser of plants, Herbert.‡ But none of these distinguished observers appear to have been sufficiently impressed with the

* 'Die Befruchtung der Blumen,' 1873, p. 4. His words are: "Es ist merkwürdig, in wie zahlreichen Fällen Sprengel richtig erkannte, dass durch die Besuchenden Insekten der Blüthenstaub mit Nothwendigkeit auf die Narben anderer Blüthen derselben Art übertragen wird, ohne auf die Vermuthung zu kommen, dass in dieser Wirkung der Nutzen des Insektenbesuches für die Pflanzen selbst gesucht werden müsse."

† 'Philosophical Transactions,' 1799, p. 202.

‡ Kölreuter, 'Mém. de l'Acad. de St. Pétersbourg,' tom. iii. 1809 (published 1811), p. 197. After showing how well the Malvaceæ are adapted for cross-fertilisation, he asks, "An id aliquid in recessu habeat, quod hujuscemodi flores nunquam proprio suo pulvere, sed semper eo aliarum suæ speciei impregnentur, merito quæritur? Certe natura nil facit frustra." Herbert, 'Amaryllidaceæ, with a Treatise on Cross-bred Vegetables,' 1837.

truth and generality of the law, so as to insist on it and impress their belief on others.

In 1862 I summed up my observations on Orchids by saying that nature "abhors perpetual self-fertilisation." If the word perpetual had been omitted, the aphorism would have been false. As it stands, I believe that it is true, though perhaps rather too strongly expressed; and I should have added the self-evident proposition that the propagation of the species, whether by self-fertilisation or by cross-fertilisation, or asexually by buds, stolons, &c. is of paramount importance. Hermann Müller has done excellent service by insisting repeatedly on this latter point.

It often occurred to me that it would be advisable to try whether seedlings from cross-fertilised flowers were in any way superior to those from self-fertilised flowers. But as no instance was known with animals of any evil appearing in a single generation from the closest possible interbreeding, that is between brothers and sisters, I thought that the same rule would hold good with plants; and that it would be necessary at the sacrifice of too much time to self-fertilise and intercross plants during several successive generations, in order to arrive at any result. I ought to have reflected that such elaborate provisions favouring cross-fertilisation, as we see in innumerable plants, would not have been acquired for the sake of gaining a distant and slight advantage, or of avoiding a distant and slight evil. Moreover, the fertilisation of a flower by its own pollen corresponds to a closer form of interbreeding than is possible with ordinary bi-sexual animals; so that an earlier result might have been expected.

I was at last led to make the experiments recorded in the present volume from the following circumstance.

For the sake of determining certain points with respect to inheritance, and without any thought of the effects of close interbreeding, I raised close together two large beds of self-fertilised and crossed seedlings from the same plant of *Linaria vulgaris*. To my surprise, the crossed plants when fully grown were plainly taller and more vigorous than the self-fertilised ones. Bees incessantly visit the flowers of this Linaria and carry pollen from one to the other; and if insects are excluded, the flowers produce extremely few seeds; so that the wild plants from which my seedlings were raised must have been intercrossed during all previous generations. It seemed therefore quite incredible that the difference between the two beds of seedlings could have been due to a single act of self-fertilisation; and I attributed the result to the self-fertilised seeds not having been well ripened, improbable as it was that all should have been in this state, or to some other accidental and inexplicable cause. During the next year, I raised for the same purpose as before two large beds close together of self-fertilised and crossed seedlings from the carnation, *Dianthus caryophyllus*. This plant, like the Linaria, is almost sterile if insects are excluded; and we may draw the same inference as before, namely, that the parent-plants must have been intercrossed during every or almost every previous generation. Nevertheless, the self-fertilised seedlings were plainly inferior in height and vigour to the crossed.

My attention was now thoroughly aroused, for I could hardly doubt that the difference between the two beds was due to the one set being the offspring of crossed, and the other of self-fertilised flowers. Accordingly I selected almost by hazard two other plants, which happened to be in flower in the greenhouse, namely, *Mimulus luteus* and *Ipomœa purpurea*, both of which, unlike the Linaria and Dianthus, are highly self-fertile if insects are excluded. Some flowers on a single plant of both species were fertilised with their own pollen, and others were crossed with pollen from a distinct individual; both plants being protected by a net from insects. The crossed and self-fertilised seeds thus produced were sown on opposite sides of the same pots, and treated in all respects alike; and the plants when fully grown were measured and compared. With both species, as in the cases of the Linaria and Dianthus, the crossed seedlings were conspicuously superior in height and in other ways to the self-fertilised. I therefore determined to begin a long series of experiments with various plants, and these were continued for the following eleven years; and we shall see that in a large majority of cases the crossed beat the self-fertilised plants. Several of the exceptional cases, moreover, in which the crossed plants were not victorious, can be explained.

It should be observed that I have spoken for the sake of brevity, and shall continue to do so, of crossed and self-fertilised seeds, seedlings, or plants; these terms implying that they are the product of crossed or self-fertilised flowers. Cross-fertilisation always means a cross between distinct plants which were raised from seeds and not from cuttings or buds. Self-fertilisation always implies that the flowers in question were impregnated with their own pollen.

My experiments were tried in the following manner. A single plant, if it produced a sufficiency of flowers, or two or three plants were placed under a net stretched on a frame, and large enough to cover the plant (together with the pot, when one was used) without touching it. This latter point is important, for if