E.—Cross and Self-Fertilisation in Plants.

CHAPTER XXII.

(1) *Introduction and* (2) *Experiments.*

FOR the full understanding alike of this work and of any account thereof, it is essential that the reader keep in mind the chief facts in connexion with the structure and functions of flowering plants, those that possess stamens and carpels. The stamens or small threads within the petals of a flower are the male organs. Within their caps or anthers is the yellow dust or pollen, of many grains. These are the fertilising structures. The carpels, generally welded together into one solid central organ of the flower, are the female organs. Within their swollen bases are the ovules or unripe seeds. These are the structures to be fertilised. Originally the fertilisation of an ovule by a pollen-grain was supposed to occur within the limits of an individual flower. Pollen of flower A impregnated ovule of flower A. And this action, whenever it does occur, is self-fertilisation. But the labors of Darwin, Gärtner, and Kölreuter, aided by the less continuous observations of others, have established that this method is a rare one. Many times more frequently the pollen of flower A impregnates the ovule of flower B of the same species. And this action is cross-fertilisation. The object of the work on plants now claiming consideration is the comparison of the effects of self and cross-fertilisation. It deals incidentally with the relative frequency of the two methods and with the means whereby each is performed, but "we are not here concerned with the means but with the results of cross-fertilisation." Speaking generally those results are advantageous to the plant in the life-battle. This work is in short "the complement of that on Orchids." In the consideration of it I shall follow the lines marked out for me by its author and deal with its introduction, the results of his experiments, the means of cross-fertilisation, the relation of insects to the process and a general summary.

(1.) *Introduction.*—This brief prelude to the main body of the work falls into four parts. (*a*) The object of the work, already discussed in the preceding paragraph. (*b*) The method of the experiments. A plant or two or three plants of the same variety was, or were, placed under a net that was not in contact with it or them. Insects were thus excluded, with the exception of one minute, experiment-disturbing being called Thrips which refused to be kept out by any net, no matter how fine were the meshes. Flowers upon this enclosed plant were fertilised, some by the pollen of their own stamens, others by pollen from the stamens in flowers on another plant of the same variety outside the net. In the former case self-fertilisation occurred : in the latter cross-fertilisation. The seeds thus produced were never gathered until they were thoroughly ripe. The seeds that were the result of self and cross-fertilisation were then allowed to germinate under exactly similar conditions. If any of the one set began to develop before any of the other, they were thrown away. But when a seed the result of the one process and a seed the result of the other began to germinate at the same time the two were planted side by side under exactly similar conditions. If any individual plant from any cause sickened in its youth, it and its companion of the opposite order were thrown away. And thus two sets of plants of the same variety, grown under exactly similar conditions, but one moiety of them the results of self-fertilisation, the other the results of cross-fertilisation, were growing side by side for comparison. Descendants of these plants of the first generation were treated as their immediate parents had been, and this process was continued even to the tenth generation in many cases. The experiments as a whole extended over a period of eleven years, a sufficiently long period to eliminate any accidental sources of error due to the circumstances of a special period of time.

(*c*) The tables. A series of elaborate tables were drawn up, month by month and year by year. In these were recorded the numbers of the flowers crossed or self-fertilised, and the heights of their offspring when measured at certain definite times from the commencement of their existence as separate individuals. The average height of the plants developed from cross-fertilised seeds was always taken as 100, and then the average height of the plants developed from self-fertilised seeds was easily comparable therewith. In any numbers I may give to afford a general idea of the results of these experiments, the 100 and its fellow numeral will be used. Not only were the heights of the flowers compared, but also the number of the ripened fruits they produced, and the number of the ripe seeds in each fruit. In all these respects, and in certain others, the plants that were the result of cross-fertilisation had, in almost every case, a very marked advantage over those the result of self-fertilisation. They were taller, they were healthier, they were stronger, they produced more fruits, they produced more seeds, they were in all ways better fitted than their fellows for the life-struggle.

(*d*) The reason of this superiority. This would seem to be that the crossed individuals possessed slight differences in their natures, as results of their having been exposed to slightly different external conditions. Those somewhat different natures have left their mark upon the reproductive structures. The pollen-grain of plant A and the ovule of plant B differ more one from the other than do the pollen-grain of A and the ovule of A, or the pollen-grain and ovule of B. With the blending of two structures somewhat different in their antecedents, and therefore in their tendencies, comes the greater possibility of further development and renewed strength. The collision of two structures thus dissimilar sets old forms of motion into stronger action, or evolves new and often unexpected forms. Hence cross-fertilisation is, moreover, of value as giving more possibility, not only of greater strength, but of variation. The whole of this important subject is dwelt upon at greater length in the present writer's "Biological Discoveries and Problems."

(2.) *Results of the experiments.*—The chapters from the second to the seventh are devoted to the description of experiments on various plants, and the tabulation of the results as far as the number of fruits, the number of seeds, and the heights of the offspring are concerned. The experiments range over thirty natural orders of plants, over fifty-two different genera belonging to those orders, over fifty-eight species. The total number of plants that were bred, watched during their development, and measured, was 2,004. The mere numbers give us some idea of the indefatigable, pains-taking nature of our teacher, whilst the fact that the observations not only extend over so many individual plants, but also have to do with no less than thirty natural orders, encourage us to believe that any generalisation based upon these experimental results must be well founded.

(*a*) Height. In Chapter II. Charles Darwin narrates fully the history and results of his experiments upon one plant, a member of the order Convolvulaceæ. It is the *Ipomœa purpurea*, commonly known as the *Convolvulus major*. In this particular plant, on comparing the heights of the plants resulting from cross-fertilisation with the heights of those resulting from self-fertilisation the following numbers appear:—

Heights of plants from	C.F.	flowers as	100
,, ,,	S.F.	,,	76

To illustrate in a yet more understandable way to most of us the difference between the average heights of the plants developed from cross and self-fertilised seeds respectively it is stated "that if all the men in a country were on an average six feet high, and there were some families which had been long and closely interbred, these would be almost dwarfs, their average height during ten generations being only 4 feet $8\frac{1}{4}$ inches."

Chapters III.—VI. are occupied with experimental details more briefly recorded as to the many other plants investigated, and Chapter VII. with a summary of the whole of the preceding pages. Of that summary I have made a summary, and I find that taking the average height of all the plants resulting from cross-fertilisation as 100, that of all the plants resulting from self-fertilisation is 87.

Two other points remain for discussion in connexion with these experiments. Thus far we have only compared self-fertilised plants with those cross-fertilised by pollen taken from plants of the same variety growing in the vicinity of the netted plants. Two other kinds of experiments were made. (i.) Flowers on the same plant were crossed, not flowers on distinct individuals. Suppose two individual plants A and B fixed by separate roots in the common earth. If A bear flowers a, a_1, a_2, and B bear flowers b, b_1, b_2, the former case was as when pollen from *b* went to the ovules of *a*. But this new case is as when pollen *e.g.* from *a* went to the ovule of a_1 or of a_2. Vigor of offspring springs not from mere crossing, but from the parents having been in slightly different conditions, for when the offspring due to this narrowed cross-fertilisation are compared with the offspring due to self-fertilisation (pollen of *a* to ovule of *a*) the *former* are the inferior. If 100 represented as before the average height of the cross-fertilised, 124 represented that of the rigidly self-fertilised! (ii.) Flowers were fertilised by pollen brought from plants of the same variety that grew at a distance from the one that was impregnated and had therefore been subject to external conditions even more distinct from those of the fertilised plant than the external conditions of any other growing in the same locality as the latter. Using our latter illustration again; whilst in the first experiments *a* flower, of plant A, was crossed by pollen from *b* flower, of B, and in the experiment just narrated *a* flower, of plant A, was crossed with pollen from a_1 flower, of the same plant A, and whilst in both these experiments the results were compared with the results of crossing ovule of *a* with pollen of the same flower *a*, in this last instance a new plant C of the same variety but hailing from a different locality comes into use. Pollen from flower *c* or c_1 or c_2, of plant C, growing perhaps in a different country is brought to the ovule of flower *a*, of plant A, and the result of this yet wider-reaching cross-fertilisation as compared with that of the cross-fertilisation between flowers of A and B that have long grown side by side and long been subject to like external conditions, is very striking. Plants springing from the ovules of plants growing at Beckenham that were crossed with pollen from some that grew at Colchester (pollen from *c* to *a*) had average height 100. Plants springing from an ordinary local cross (pollen from *b* to *a*) had average height 78. These Colchester plants had grown up with different surroundings from those of their Beckenham congeners and the nature of the former differed slightly from that of the latter. With the blending of two structures somewhat more different in their antecedents and therefore in their tendencies comes the yet greater possibility of further development and renewed strength.

(*b*) Fertility. The study of the relative fertility of different flowers as influenced by cross and by self-fertilisation includes two questions. (i.) As to the productiveness of flowers fertilised by their own pollen or by that from another plant. (ii.) As to the productiveness of the seedlings raised from the former set. The two classes of cases do not always run parallel. (i.) The comparative fertilities under this head were measured by counting the number of fruits produced and the number of seeds contained by those fruits of the cross and self-fertilised flowers. A series of experiments upon the same plants as those whence the height-data were obtained, resulted in the following numbers:—

Number of	fruits	formed by	C.F.	flowers,	100
,,		,,	S.F.	,,	69
,,	seeds	,,	C.F.	,,	100
,,		,,	S.F.	,,	93

A yet more elaborate series of experiments wherein the fertility of plants was estimated by various methods are expressed in a numerical table that may be summarised thus. Take the fertility of the cross-fertilised flowers as 100, the average fertility of all the self-fertilised is almost exactly 60.

This investigation of the relative productiveness of flowers leads to the account of plants that are absolutely self-sterile. Kölreuter had shown long ago that the flowers of *Verbascum phœniceum* (one of the Mulleins) were sterile with their own pollen, and Fritz Müller, most earnest of helpers in that propagandist work of evolution that consists in fact-finding, had discovered that on the stigmas of certain Orchids pollen from the stamen in the same flower acted as a poison. Other observers have shown that the number of plants whose ovules cannot be ripened by the pollen of the same flower is large, and the same observations that have established these facts have demonstrated in addition that this self-sterility is determined by external conditions, these same external conditions rendering the male and female sexual organs and elements too uniform for interaction one upon the other. Self-sterility would seem to have been gradually acquired through natural selection as it would be a preventive to self-fertilisation with its attendant evils, negative or positive.

But the discoverer of the fact of natural selection with his customary honesty urges certain objections to this view. (α) The absence of connexion between the sterility of self-fertilised parent-plants and the loss of vigor in the offspring of such plants. (β) Individuals of the same parentage differ in the degree of their self-sterility. (γ) The effect of mere alteration in external conditions in causing self-sterility. (ii.) The productive power of seedlings resulting from cross-fertilisation is also far greater than that of seedlings resulting from self-fertilisation.

(*c*) Differences other than those of height or fertility. The eighth chapter of the book deals with other advantages possessed by the plants that are the result of cross-fertilisation in greater degree than by those that are the result of self-fertilisation. These are three in number: (i.) greater strength (ii.) earlier flowers, (iii.) greater diversity of color.

(i.) Greater strength. Dealing with certain specimens of *Viola tricolor*, the common heartsease, in 1870, Darwin observed that from the great severity of the winter of that year all the offspring of self-fertilised ovules were slain, with the pathetic "exception of a single branch on one plant, which bore on its summit a minute rosette of leaves about as large as a pea." All of them were killed by the frost. But the cross-fertilised to a plant arose strong and living in the spring-tide of 1871. And as a general conclusion it is stated that whenever the experiments required the removal of the plants from the fostering comfort of their early home, the greenhouse, to the harsher world outside, the cross-fertilised children bore up better than the self-fertilised ones. These last also were more liable to premature death, weaklier infants that they were, than their stronger fellows. Of the many cases when two plants were doomed to be thrown away in their earliest hours, the majority were due to the failing of a self-fertilised little one, its weakness with a strange irony bringing about the destruction not alone of itself, but of one more worthy.

(ii.) Earlier flowering. The results of cross-fertilisation were generally earlier in their upspringing towards the sun than the self-fertilised. Thus 58 cases are on record of the periods of flowering on the part of a number of plants of both kinds. In 44 of the 58 the crossed plant flowered first; in 9 of the 58 the self-fertilised plant flowered first; in 5 there was a dead heat.

(iii.) Greater diversity of color. Given original parent plants of varied hue, and from these careful breeding both by method of self and of cross-fertilisation, it is observable after a certain number of fertilisations that the offspring of self-fertilisation become uniform in color, losing all diversity of marking and of tint, while the offspring of cross-fertilisation retain or even add to the primal variegation of color. Crossing of the uniformly-painted, self-fertilised plants with a fresh stock results in seedlings reverting to the diversified arrangement at first prevailing.

Summing up these consequences of cross-fertilisation and self-fertilisation we have (α) The greater physical strength of the seedlings that are the result of cross-fertilisation, giving them far more chance of survival during the earlier and dangerous hours of life, and fitting them in succeeding hours and days to encounter alterations of external conditions of considerable magnitude without succumbing. (β) Their superior height lifting them into air regions whither their weaker brethren cannot follow them, and yielding to breathing and feeding leaves ever greater opportunities of air and food. (γ) Earlier flowering, a distinct advantage when fertilisation depends upon active insects who are most active in the younger summer months. (δ) More diversity of coloring, therefore greater attraction of insects, and greater chance of fertilisation through insect agency. (ϵ) More numerous fruits each containing (ζ) more numerous seeds than are produced by the self-fertilised plants. In all directions, then, advantage and better hope in the battle of living things. Cross-fertilisation is clearly of greater value to its possessor than self-fertilisation. And it must never be forgotten that this same help-giving cross-fertilisation carries with it as inevitable and irresistible corollary, variation, and is therefore by its frequency and its effect strongest of arguments in favor of evolution.

CHAPTER XXIII.

(3) *Means of Fertilisation*, (4) *Sexes in Flowers*, (5) *Summary*, *and* (6) *The Writer.*

(3) *MEANS OF FERTILISATION.*—(*a*) In Cryptogamia. In the Algæ, the Characoæ, the Ferns and their allies the male element is generally very mobile. The antherozoids of these lowest plants are usually provided with cilia, and whether thus furnished or not are almost invariably capable of considerable movement. Hence transportation of these male elements from place to place, and the probability of fertilisation of a female element belonging to a plant other than that whence the antherozoid came. And this would be a case of cross-fertilisation. (*b*) Phænogamia. In the higher sub-kingdom of flowering plants or Phænogamia, whose members have pollen and ovules, two types of plants occur. (i.) Anemophilous plants (ανεμος = wind, φιλεω = I love). These are plants such as the plantain, the oak, the grasses, whose multitudinous, incoherent pollen grains are borne by the wind from flower to flower. By such an arrangement as this cross-fertilisation is again rendered well-nigh certain, and the fact that amongst anemophilous plants the male and female organs are generally in separate flowers, and very often on separate plants, points to the same method of impregnation. (ii.) Entomophilous flowers, or those whose pollen is borne from flower to flower by insects. As arguments in favor of cross-fertilisation of such plants as these Charles Darwin urges: (α) That insects do thus transfer the fertilising element from flower to flower. (β) That some birds perform the same function. The humming birds and the lories seem to be the busiest at this work. (γ) That many plants are dioicous (δις = twice, οικος = house) *i.e.*, the male flowers are on one plant, the females on another. (δ) That others that are not dioicous are monoicous and diclinous, *i.e.*, both male and female flowers are on the same

plant ($\mu o \nu o s$ = one, $\grave{o}\iota\kappa o s$), but yet the flowers are either male or female, and never with both sexes combined on the same individual blossom ($\delta\iota s$, $\kappa\lambda\iota\nu\eta$ = bed). (ϵ) That even when plants are bisexual and each flower carries both male and female organs, yet the flowers are dichogamous ($\delta\iota\chi o s$ = double, $\gamma\alpha\mu o s$ = marriage). The male and female organs of any particular flower are not ripe and ready for interaction at the same time. Generally the stamens are ready for work before the carpels. Most plants are proterandrous ($\pi\rho o\tau\epsilon\rho o s$ = former, $\dot{\alpha}\nu\eta\rho$ = man). When, therefore, pollen of flower A is ready, the ovules of flower A are not ready. But those of B, an older flower of the same variety, may be ready, and by insects pollen from A may be carried to the flower of B whose ovules are ready to be impregnated thereby. (ζ) That the pollen of another plant of the same variety is prepotent over the pollen of the plant itself. If pollen from A and from B be placed simultaneously on the stigma of A when it is ripe, only the pollen of B will do work, and making its way down the canal of the style impregnate the ovule. Pollen of another kindred plant is more potent than that of the plant itself even if the latter be placed upon the stigma some hours the earlier of the two. (η) That in certain cases special arrangements of parts of the flower or special movements of parts prevent self-fertilisation. The structure of the stigma of Violet with its projecting lower lip, that closes the opening of the stigma as the proboscis of the insect, covered with pollen from the same flower, is withdrawn and allows the mouth of the stigma to open as the proboscis of the insect covered with pollen from another flower enters is an instance of the former. The special movements of parts of the Orchid flowers, notably *Spiranthes*, described on page 123, is an instance of the latter.

(4) *Sexes in flowers.* Discussion as to the order of evolution of unisexual and bisexual flowers follows. Charles Darwin is of opinion that plants were originally unisexual. The male and female organs were in distinct individuals, and on separate plants (dioicous). Later certain plants were evolved, bearing male and female flowers on the same plant (monoicous). Yet later, certain plants were evolved that were bisexual, having in each flower male and female organs (hermaphrodite, from Ἑρμης = Mercury,

Αφροδιτη = Venus). To this series of evolutions it may be urged, with all deep respect for its illustrious suggester, that considerable objections exist. (*a*) It is opposed to the general principle of evolution from the general to the special. In the higher forms of living things there is more specialisation of function, more division of labor, than in the lower. Special organs are found performing special functions. From this point of view it would seem more likely that in the earlier forms both sexes were in the same individual, and later on that further specialisation took place, and each individual became either male or female. (*b*) The study of the animal kingdom affords collateral evidence against the view enunciated in this work. The lowest animals are very clearly bisexual. The highest are very clearly unisexual, though, in the similarity of the early stages of the male and female, and in occasional abnormal reversions to the hermaphrodite condition, we have evidence as to their evolution from forms originally bisexual.

Perhaps part of the difficulty in this particular case of evolution is traceable to our habit of regarding all the brightly-colored and highly-scented flowering plants as higher in the scale than their less gay and less attractive fellows. The majority of people probably would unhesitatingly vote the rose to be higher than the oak. But it is not altogether certain they would be accurate in doing thus. If color and odor and beauty only are to be the measures of excellence, the judgment may be correct. But if bulk and strength and the beauty of strength, if effect upon the air and the soil, even if complexity of structure are to be taken into account, perhaps the decision may be impugned. The writer is strongly inclined to believe that the forest trees will be regarded as higher in the scale of vegetables than the flowering herbs. And the latter are bisexual, whilst the former are unisexual.

(5) *Summary.*—The volume closes with a general summary of the work recorded and the conclusions reached. Thence I select the three main generalisations. (*a*) Cross-fertilisation is generally beneficial to the plant, self-fertilisation injurious. (*b*) The advantages of the former follow from the individual plants concerned having been subjected to somewhat different conditions; hence their sexual elements are, therefore, somewhat differentiated. (*c*) The

disadvantages of the latter follow from the sexual elements in the same plant not having been thus differentiated.

"There is the clearest evidence, as we shall presently see, that the advantage of a cross depends wholly on the plants differing somewhat in constitution, and that the disadvantages of self-fertilisation depend on the two parents, which are combined in the same hermaphrodite flower, having a closely similar construction. A certain amount of differentiation in the sexual elements seems indispensable for the full fertility of the parents and the full vigor of the offspring."

(6) *On the writer of the book.*—From this volume, as from all the rest, we can gather some faint hints as to the nature of its writer. (*a*) It is curious to note how the old phraseology of teleological explanation is still at times used. (i.) The phrase "in order that" occurs more than once. Thus, on page 372, we have:—"Almost every fruit which is devoured by birds presents a strong contrast in color with the green foliage, *in order that* it may be seen, and its seeds freely disseminated."

Ten pages further on we read:—"It may be admitted as almost certain that some structures, such as a narrow elongated nectary, or a long tubular corolla, have been developed *in order that* certain kinds of insects alone should obtain the nectar." And on page 385:—"We are thus led to infer that some plants either have not had their flowers increased in size, or have actually had them reduced and purposely rendered inconspicuous, so that they are now but little visited by insects."

(ii.) The word "instinct" occurs on page 415: "Their instincts, however, are not of a specialised nature, for they visit many *exotic* flowers as readily as the *endemic* kinds, and they often search for nectar in flowers which do not secrete any; and they may be seen attempting to suck it out of nectaries of such length that it cannot be reached by them."

The researches of so many naturalists, as recorded in Büchner's "Mind in Animals," translated by Mrs. Besant, have done so much to show that the word "instinct" is in many cases, if not in all, to be replaced by "education"—that the former word should be very cautiously used if it be employed at all, and may not improbably ere long pass out of our vocabulary.

(iii.) "The economy of Nature." I venture to think this phrase is very misleading, especially when used by one whose words carry so much power as those of Charles Darwin. It is seriously open to question whether that economy exists to any large extent. In many instances the most extensive waste is evident in Nature. A case may be mentioned from this very work. Two pages after the one (374) wherein we read: "So great is the economy of Nature," the following sentence occurs: "The Editor of the *Botanical Register* counted the ovules in the flowers of *Wistaria sinensis* and carefuly estimated the number of pollen-grains, and he found that for each ovule there were 7,000 grains." As at most three or four pollen-grains are enough to fertilise an ovule and as in many cases one will do the work, Nature cannot be accused of economy here. The whole history of anemophilous flowers with their crowds of pollen grains wafted in every direction by the wind and only a few here and there ever reaching a stigma and functioning as impregnators, and the huge waste of the eggs, say of fishes, millions of which never develop, are but two cases of the many that might be educed to show that in Nature waste is very prevalent.

(*b*) The marvellous labor of perseverance again shines out. The mere seed-counting alone involved immense toil. *Ex uno disce omnes.* "Fifteen capsules from self-fertilised cleistogene flowers contained on an average sixty-four seeds, with a maximum in one of eighty-seven." Not only were the heights of innumerable plants carefully measured and recorded, but to leave no stone unturned in the investigation as to their relative vigor in the latter experiments, the fully-grown plants were cut down and weighed.

Again on page 179: "On one of these plants several flowers were fertilised with their own pollen; and as the pollen is mature and shed long before the stigma of the same flower is ready for fertilisation, it was necessary to number each flower and keep its pollen in paper with a corresponding number."

After meeting passages such as these wherewith the work abounds one reads with a half-smile "It was too troublesome to collect and count the capsules on all the plants."

(*c*) The intense honesty of one who only labors to find out what *is*, comes out frequently, and evidently with a total unconsciousness, in these pages. Thus on page 128 he writes: "The results of my experiments on this plant are hardly worth giving, as I remark in my notes made at the time, 'seedlings, from some unknown cause, all miserably unhealthy.' Nor did they ever become healthy; yet I feel bound to give the present case, as it is opposed to the general results at which I have arrived."

And again on page 185: "But many of the plants were unhealthy, and their heights were so unequal—some on both sides being five times as tall as the others—that the averages deduced from the measurements in the preceding table are not in the least trustworthy. Nevertheless I have felt bound to give them, as they are opposed to my general conclusions."

(*d*) Ever and anon also a glimpse comes into the personal nature of the author. References to his sons' work, that of Francis and of George, meet us pleasantly.

Sometimes there is an anxiety that is almost childlike. When one reads: "In my anxiety to see what the result would be, I unfortunately planted the three lots of seeds (after they had germinated on sand) in the hothouse in the middle of winter, and in consequence of this the seedlings (twenty in number of each kind) became very unhealthy," one is half-reminded of the boy who planting cherry seeds, daily dug them up to see how they were getting on. When an extraordinary plant that though the result of self-fertilisation yet outgrew the ones that were the result of cross-fertilising is encountered, in the exuberance of his surprise he names it "Hero." Good, gentle, kindly, patient man, working serenely on. It is well for us that we have even such fragmentary glances as this at the great life that has made and shall make so many lives the happier and the nobler.

And throughout the work is visible the patient joy of the experimenter and at intervals the triumph, than which none is more sacred, of him that out of many facts draws the one large truth and offers it to the eyes of his fellows and of after-time.