## 28.—The Fertilisation of Plants.

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I purpose giving you this evening a short account of a new work by Mr. Darwin. As you are all doubtless aware, whatever he undertakes he does thoroughly, and his book on "The Cross- and Self-Fertilisation of Plants," which came out last January, contains observations upon experiments he has been making for several years past. It is a book that takes, I had almost said months, certainly weeks, to digest thoroughly; and although no one can gainsay the majority of his conclusions, there is one point from which, I think, he has drawn a wrong inference; and I shall comment upon it. I mean "Self-Fertilisation." My first idea was to make that the subject of this lecture, but I shall take the whole question, and then put before you wherein I think lies his mistake, and I shall be very glad if any one will criticise my views.

It is just two hundred years ago since Sir Thomas Millington detected the use of the pollen for the fertilisation of the stigma. As soon as that necessity was recognised, the idea very soon followed that flowers were adapted to secure their own seeds by the pollen falling on the stigma of the same flower. I think it was Linnæus to whom is attributed the statement that both pendulous and erect flowers have the stigmas *below* the anthers, so that the pollen may fall from the latter upon them. Further observations would have shown that this is not universally true. Take, for instance, the common crocus. In the purple variety the stigma is erect and forms a brush, but the stamens are below it. The tops of the anthers only reach a height below the point where the stigmas branch, so that this is a case in which the rule fails. It was soon found that in many instances it would not apply, and it was also noticed that all flowers had not both stamens and pistils in the same flower, *e.g.* cucumbers and melons; and similarly with regard to several trees, such as the willow; so that it was clear there must be some other law than that the pollen should fall on the stigma of the same flower. Hence "intercrossing" was suspected, and Sprengel, a German, in 1790, wrote a very interesting book, in which he noticed a great many plants, the pollen of which it is necessary for insects to carry from one flower to another. We have, however, to thank Mr. Darwin for elucidating the fact, and establishing, on a thoroughly scientific basis, the necessity for insects to visit conspicuous flowers and carry the pollen from one to another. He was the first English botanist who established that fact, although he has had a great number of followers since; and anybody who searches regularly into flowers is pretty sure to find some new contrivance. I will mention one of a few recorded by myself, viz. that of the crocus. As soon as the bees come out in spring, you can easily see how they succeed in intercrossing this plant. The perianth of the crocus is contracted at the base, so that if the bee alights on the inner surface of it, she cannot get down to the bottom where the honey lies, and so she alights on the brush-like stigma, and goes head downwards, grasping the whole column of stamens with her legs; consequently the anthers dust the bee on the under-side with pollen. It should be noticed that the anthers do not burst inwards, as is ordinarily the case in flowers, but outwards, so that the bee smears herself over with pollen; she then flies to another flower, alights on the brush-like stigmas, and these of course sweep off the pollen which the bee has brought. That is just an instance of the intercrossing of flowers. Mr. Darwin's work on the 'Fertilisation of Orchids' is a most interesting book, and deals with one particular family; but intercrossing occurs in nearly all orders of the Vegetable Kingdom.

Having thus detected that the pollen was necessary to fertilise the pistil, intercrossing was looked upon to some extent as a necessity. It was a sort of general surmise that plants produced by the resulting seeds were benefited if the pollen had come from any other flower than its own; but the *exact value* was never known; and it is remarkable that Dean Herbert, in his work on the *Amaryllideæ* (1836) says: "I am inclined to think I have derived advantage from impregnating the flowers from which I wish to obtain seeds, from individuals of another variety or another flower rather than its own, and especially of any grown in different soil or aspect." That is a remarkable sentence, and we have been forty years without having this fact established, so that the great value of Mr. Darwin's new book lies in the fact that it gives us the exact value of these three kinds of crossing.

Let us, then, start from this point, and we will take four kinds of combination. The first is when the pollen of flowers falls on their own stigmas: that is self-fertilisation. The second kind of union is that of crossing different flowers, but on the same plant. The third is the intercrossing plants of the same stock, grown in the same garden, and sprung from the same ancestor, and consequently all of close kinship. Lastly, there is the crossing plants from distinct stocks; one, say, growing in Mr. Darwin's garden, and the other brought from Colchester or elsewhere, and of course grown under different circumstances.

Mr. Darwin went through an elaborate series of experiments on fifty-four species of thirty distinct natural orders, and I will give you the main results. The first case upon which he experimented he carried out more fully than all the others. He cultivated the so-called "Convolvulus major" (*Ipomœa purpurea*) for ten years, year by year, and his method was to fertilise the flowers artificially with their own pollen, and collect the seeds from those flowers: he called them "self-fertilised seeds." On the other hand, he fertilised the flowers of plants with the pollen of other flowers growing in his garden, and called the result "intercrossed seeds." Then he allowed both kinds to germinate, and as soon as he got pairs of exactly the same height, he planted them on opposite sides of a pot, the mould and moisture, etc., being the same, and the plants subject to exactly the same conditions. Then he allowed these pairs to grow up, and when they were fully grown he measured their heights in inches, always calculating the "intercrossed" as 100 for convenience, and the resulting ratios were recorded for ten years. He grew five or six pots every year, and in each pot five or six pairs of plants, thus raising an immense number of plants altogether. He added up the heights, and then divided by the number of plants, so as to get the average. In the first year's growth the heights were as 100 to 76; 100 representing the "intercrossed" and 76 representing the self-fertilised. It went down to 68 the third year; and in every year the self-fertilised fell short of 100. The interpretation of this, therefore, was that intercrossing did a great deal of good, as shown by the "intercrossed plants" being higher than the "self-fertilised." Grouping the years in threes, another result comes out. Thus the averages of the first three years give the ratio of 100 to 74. The averages of the fourth, fifth, and sixth years give the ratio of 100 to 78, *i.e.* they are nearer equality; and the average of the next three years gives the ratio of 100 to 88, *i.e.* still nearer equality. *Hence the ratio is becoming approximately equal to unity as the generations go on.* It shows however that the intercrossing was beneficial for the first few years, but as it proceeded the benefit apparently began to die out, and the plants became approximated to the self-fertilised. You get the very same result when you take the ratios of fertility, as represented by the average number of seeds developed in the capsule. Mr. Darwin has not tabulated this, but I have calculated it from his book. There are two generations in the proportion of 100 to 93; the next two generations are as 100 to 94; one generation, the fifth, gives a ratio of 100 to 107, while the eighth gives a ratio, by calculation, of 100 to 114! Hence there is a gradual approximation to unity, or 100 to 100, as years go on, in two respects. Intercrossing appears to be beneficial at first; but afterwards the benefit dies out, and then the plants show no improvement upon the self-fertilised. On the contrary, self-fertilisation proves to be more beneficial than intercrossing.

This is also shown in another way. When Mr. Darwin first cultivated the plants, there was an immense variety in the colours; but subsequently they got less variable, the intercrossed gradually assumed one and the same colour, though never absolute uniformity; whereas the self-fertilised became absolutely uniform in colour. This brings out an important horticultural fact. If a gardener wishes to keep any particular strain, he must be very particular not to cross it by another strain, but propagate it either by slips, bulbs, etc., or *self-fertilise it*, for such fixes the colour.

We will now consider the crossing of flowers on the same plant. Unfortunately Mr. Darwin has not gone into this so fully, and one cannot therefore draw very safe deductions from his experiments;

but the conclusion, as far as it goes, appears to be this. He tried first of all the *Ipomæa purpurea*, and found the relative heights of plants grown from seed of the intercrossed flowers on the same plant, to the self-fertilised, were as 100 to 105. That showed it was better for a flower to be self-fertilised than to be crossed with another flower on the same plant. He cut down both the self-fertilised and crossed plants, *i.e.* those which had been the result of a seed of flowers fertilised respectively as stated, and the ratio of their weights was as 100 to 124, so that in height and weight it showed that the self-fertilisation was better than the crossing. This was a different result from what was anticipated. Botanists had been inclined to take it for granted that it was always beneficial to cross flowers even on the same plant, as Dean Herbert had surmised. Mr. Darwin only tried five plants. Of *Mimulus luteus* the height was as 100 to 101, and the weight 100 to 103, the benefit being on the side of the self-fertilised. *Digitalis purpurea* gave ratios 100 to 94 in height, the weight 100 to 78, showing no slight benefit in crossing the flowers. In another part of his book Mr. Darwin alludes to what some other botanists had found, viz. that no difference occurred with *Reseda*, *Dianthus*, or *Abutilon*; but a slight beneficial effect appeared in thus crossing *Eschscholtzia*, *Oncidium* and *Corydalis cava*. A curious fact is noticeable here. All the plants which derived a benefit were naturally more or less *self-sterile* plants, as stated in his list of self-sterile plants, *i.e.* which cannot naturally set seed of themselves. Therefore I think we may at least suspect, if not generalise, that the benefit derived from crossing flowers on the same plant may prove to be more or less limited to those naturally self-sterile.

Next, we must consider the effects of introducing a new stock. He did this with some half-dozen plants, and then the benefit was something very great indeed. He has given a table (C) in the book, and by tabulating the mean results of it, and taking 100 as the standard for the new stock, we arrive at the following conclusions:

| | | | | |
|---|---|---|---|---|
| Mean of | heights | of crossed to | intercrossed | = 100 : 85. |
| ,, | ,, | ,, | self-fertilised | = 100 : 75. |
| ,, | fertility | ,, | intercrossed | = 100 : 40. |
| ,, | ,, | ,, | self-fertilised | = 100 : 25. |
| ,, | weight | ,, | intercrossed | = 100 : 116. |
| ,, | ,, | ,, | self-fertilised | = 100 : 53. |

"Crossed" signifies crossed with a new stock; "intercrossed" signifies crossed with the same stock.

You see that in this table nearly all these numbers are considerably less than 100, showing as a rule that the benefit derived from crossing with a new stock, whether in height, weight, or fertility (estimated by the number of seeds), is immense. But it is not absolute—there are exceptions, and the number 116 stands out as an exception. That, however, is the mean of only three plants, too few from which to generalise.

I will enumerate some of the benefits which Mr. Darwin observed;

although you cannot generalise from these effects, yet they occurred in individual cases, where the crossed plants showed some special or particular advantage in other respects than height, weight, and fertility; for example, on one occasion he planted the self-fertilised some hours, or even a day or two before the others, and then the crossed overtook them and beat them in the race. Then he found they were better able to resist unfavourable conditions of various kinds: such as a sudden removal from the greenhouse to the open ground, which checked the self-fertilised, whereas the others were able to stand it. But this was only in particular instances. They also better withstood cold and intemperate weather, and a severe frost on one occasion. The period of flowering of the intercrossed was earlier than that of the self-fertilised, sometimes days, or even, as in the case of *Cyclamen*, three weeks. To sum up the results, we find that the experiments establish these main facts. By introducing a new stock, the cross benefits the plants in every way, they grow higher, their leaves are larger and greener, and they become altogether finer and more bushy plants, and produce a greater profusion of flowers, while the flowers are subject to greater variations of colour. Secondly, by intercrossing two plants of the same stock, you get a certain amount of benefit, but in a lesser degree; but if one continues to cultivate the same stock year after year, the benefit derived at first gradually disappears, the plants finally become as if they fertilised themselves, and the flowers retain the same uniform colour.

Then we come to the process of self-fertilisation. We have considered the three kinds: a distinct cross, *i.e.* with different stock; crossing the same stock; and crossing flowers on the same plant; but self-fertilisation is the subject on which I join issue with Mr. Darwin. Throughout the book he uses the phrases "evil effects of," and "injurious effects of," in regard to self-fertilisation. Of course he has proved the benefits of crossing; but to say that the opposite process is "injurious" is, I think, misleading. For when you read of "injurious effects" you infer some unhealthiness or infertility. Cases amongst cultivated plants may occur where something like "injurious effects" may be recognised, but apart from individual and exceptional cases, to lay it down as a broad general rule is, I think, erroneous. Mr. Darwin heads a section on p. 303 as follows:—"On the preservation of the good effects from a cross and the evil effects from self-fertilisation." But out of the seventy-four cases he has cultivated, he has only got three plants to bring forward. The first one, *Nemophila insignis*, must be struck out altogether, because he says: "This experiment was quite worthless." That reduces us to two cases only. One is the common pansy, and the way in which he wished to show the benefit was by taking two plants cultivated for one generation; the one crossed, the other self-fertilised, and the ratio of the two was as 100 to 42, showing a very great benefit to the intercrossed. He now crossed the seedlings of *both* of these two; and he thought the one doubly-crossed would show the transmitted benefit and be thus superior to the (now crossed) self-fertilised. It did, as the ratio, 100 to 82, indicates. This is nearer to unity than before, but it only shows that the self-fertilised plant was now benefited by its being crossed, while the (twice) intercrossed retained some benefit, but did not acquire any proportionally increased advantage. The next was the sweet pea. In the first generations, the intercrossed to the self-fertilised was 100 to 80, the next year 100 to 88. Then he allowed *both* to be *self-fertilised*, and the ratio was 100 to 90, or nearly 90. Then, he says, some were cultivated in very unfavourable situations, and showed in an "unmistakable manner" the superior constitutional vigour in those which had been intercrossed. He put some in a pot containing a large *Brugmansia*, and in poor soil, and the ratio was 100 to 88, *exactly that of the previous year*. Again, when planted on poor soil in the shrubbery, others reached 100 to 98, or practically showing no difference between the intercrossed and self-fertilised, *i.e.* the benefit of intercrossing was *not* transmitted. So from these two cases I do not see that he is justified in attributing "evil effects to self-fertilisation." He established the fact that the benefits of the cross may be handed down, but the "evil effects" of self-fertilisation are not proved. The self-fertilised were just as healthy. He remarks that both produced a profusion of pods, and, in fact, under the shrubbery they were practically equal in height.

He adds a remarkable instance, where he says the effect of the cross was carried on for a long period. A variety of the common pea was raised by Mr. Knight by crossing distinct varieties, and it retained its characters by self-fertilisation alone *for upwards of sixty years*. If it was not superseded for sixty years as a marketable product, the words "evil effects" are surely misleading. The crossing has to thank the self-fertilising power of the pea for keeping it up so long!

Now I will give you what seem to me the grounds for believing in the benefits of self-fertilisation. You may think it strange after what I have been saying, but in many cases I think it is true, and Mr. Darwin himself admits it. Although he talks about the "evil effects," yet he admits that in some cases self-fertilisation must be beneficial. This was the case when the results were compared with those of crossing flowers on the same plant. The self-fertilised plants of *Ipomæa* were higher than the intercrossed. He says: "This is a remarkable fact, which seems to show that self-fertilisation is more advantageous, *unless* the crossing brings some decided and appreciable advantage." This is the clue to the whole thing. Crossing is only a means to an end, and that end is the introduction of new constitutional elements. Hence by means of intercrossing, different plants, which are living under slightly different circumstances, have new elements of constitution introduced into each other; and from this arises the benefit. The mere act of crossing does no good. It is similar or analogous to ourselves going to a different part of the country for change of air. An invalid likes change and new scenery, for they invigorate the constitution. So as long as a plant goes on fertilising itself, it cannot introduce new constitutional elements; but carry it into a new country, and you may see a surprising difference. The water-cress, which is self-fertilising, now growing in New Zealand, retains the same form that it has here, but it grows twelve feet long, and nearly an inch thick, and has increased so that the Government expends large sums every year in keeping the rivers clear of it. It is not only far superior to, but is completely driving out the native water-plants.

I will now enumerate several facts which will, I think, make out the case of self-fertilisation. 1. The majority of flowering plants are self-fertile. Mr. Darwin's book brought that out more than I suspected to be the case. The general idea was that conspicuous flowers are adapted solely for intercrossing. That is not quite true; though a large number of conspicuous flowers are strongly "proterandrous," that is, mature their stamens before their stigmas, and so cannot be self-fertilised; as the common clove pink; but the *Ipomœa purpurea*, which is a very conspicuous flower, though freely crossed by bees, yet will fertilise itself if we keep the bees away. 2. Very few plants are known to be physiologically self-sterile. It is a remarkable fact that some plants are in this condition; but put the pollen on another flower, and it is effective. 3. Many are morphologically self-sterile. That means, the pollen cannot reach the stigma of the same flower unless artificially put there, but it is then effective. 4. Self-sterile plants may become self-fertile by many causes. Some of these causes want a little more establishing, it is true; but they have at least been noticed in certain cases. For instance, the withering of the corolla. Mr. Darwin mentions the case of the pansy. I have noticed the same thing in plants in the autumn, when it is getting too cold for the corolla to expand. You may find the corolla withered and pressed down upon the stamens and pistil, which then seeds abundantly. Such a case I have observed in *Tradescantia*. 5. Loss of colour. That means loss of energy; because it is known that if you keep balsams without ammonia in the soil, they will be white, but with ammonia they become pink again. The conclusion I draw is that from whatever cause the energy in a plant is destroyed, its loss may be indicated by a white or pale-coloured corolla. Loss of energy appears to be favourable for self-fertilisation; but the converse is not necessarily true. In Mr. Darwin's book there are about half a dozen instances where he mentions that pale flowers and white flowers are more self-fertile than others. 6. The absence of insects. It appears that some flowers which are habitually crossed in their own country by insects, on transportation to another country, where there are none of those insects, may become self-fertilising. Three common examples are the sweet pea, the garden pea, and the dwarf kidney-bean. The pea is really adapted for insect agency, but it is self-fertilising in this country, apparently because we have not the proper insect to fertilise it. If plants therefore do not receive visits from the right insects, the probability is that they will generally die out, and we have reason to suppose that many have died out on that account; but the pea and others may be regarded as exceptions which have become self-fertilising instead. 7. Highly self-fertile forms may arise under cultivation. In cultivating the *Ipomæa purpurea* for three years, not one single plant of the self-fertilised appeared taller than the crossed; in every individual case the intercrossed was taller than the self-fertilised; but in the third generation one plant grew to a greater height, and Mr. Darwin says he was so much surprised that he saved the seed to see what would happen. However, it only beat its competitor by ·6 p.c., that is, the ratio of the intercrossed to the self-fertilised was 100 to 100·6; which is practically one of equality. He called that plant "Hero," and saved the seed, to see whether the seedlings would show any tendency to be taller than the intercrossed. The descendants did exert a power of growth quite equal to the ordinary intercrossed, and became more fertile than is usually the case, for they had a higher average of seeds per capsule than in any other cases. No benefit followed from intercrossing, and not even any benefit from crossing with new stock! So that this was a very remarkable individual, for its descendants had great self-fertilising powers and always beat their competitors. When one studies the details of the experiments with the different species, there is scarcely a single table where there are not three or more self-fertilised seedlings which beat their competitors. So that Hero was not by any means an exceptional case of a self-fertilised plant growing taller and being more vigorous than the others. Indeed it seems to have been a very common thing indeed. Hero was the first, and therefore Mr. Darwin studied that individual. 8. Special adaptations occur for self-fertilisation. We have had so much literature on the subject of intercrossing published of late years, that the peculiarities of self-fertilisation have been rather neglected. Take, for instance, the two common mallows, *Malva rotundifolia* and *sylvestris*; the latter is a conspicuous large flowering species, and is "proterandrous," *i.e.* the stamens all shed their pollen long before the styles and stigma rise up and are ready to receive it; so that it cannot possibly be self-fertilising. *Malva rotundifolia*, on the other hand, is self-fertile: the styles rise up and are mature at the same time as the stamens. They curl backwards, inserting the stigmas amongst the anthers, and thus secure the pollen on their own stigmas, and the plant is self-fertilised. The pansy (*Viola tricolor*) does not usually set seed of itself, but requires to be intercrossed. It is a self-sterile plant. Hermann Müller, who has especially studied these conditions, found some very small and inconspicuous varieties, in which the stigma was turned towards the stamens, and received the pollen directly from them. It will be found to be a general rule that small inconspicuous forms are self-fertilising, while larger and brightly-coloured flowers require insects. Inconspicuous flowers are therefore probably always self-fertile, without, however, precluding the possibility of their being crossed. I have examined a very large number of our common weeds, and I found the pollen grains always penetrating the stigma. Many of them fertilise themselves in the bud without opening at all. The common chickweed and the *Spergula arvensis* in the winter never open; but the anthers will be found clustering round the stigmas, and the flower seeding itself rapidly in that state. They fertilise themselves with great ease and great rapidity. It is astonishing how soon the seeds ripen and escape. 9. "Cleistogamous" flowers. Certain plants, besides bearing conspicuous flowers, as the common violet, have inconspicuous, almost microscopic flowers as well, which never open. Now the ordinary violet-blossoms rarely set any seed; but if you turn up the leaves in the summer, you will find a great number of minute buds, not much bigger than a large pin's head, but they often have no petals, and the stamens are reduced to two or three, and the anthers are pressed down on the stigma, and the result is that these minute flowers are self-fertilising and set seed in profusion. *Oxalis*, or the wood sorrel, is another instance; as is one of the balsams; and *Lamium amplexicaule* also has cleistogamous flowers. 10. The relative fertility may equal or surpass that of crossed plants. Very often the number of seeds per capsule did not differ much between the intercrossed and the self-fertilised in Mr. Darwin's experiments; but the intercrossed being more vigorous produced more flowers, so that the absolute fertility was very greatly in favour of the intercrossed, but the number of seeds per capsule did not materially differ. Then, again, the fertility does not decrease. If there were injurious effects in self-fertilisation, one would think that the fertility would decrease in successive generations, but it does not; and in some cases plants usually requiring to be intercrossed became very self-fertile, by the anthers maturing with the stigma instead of before them, and Mr. Darwin found the fertility then increased in successive generations. This was the case with the clove pink. 11. When the plants were grown in competition on opposite sides of the pot, so long as they were seedlings, there was no difference; but as soon as they began to increase in size, competition set in. It was with that object he put them in the same pot, to resemble the "struggle" which occurs in nature. But it is generally plants of different orders that compete together in nature, and not plants of the same kind; and two plants of totally different orders will grow together where plants of the same kind will not, for they do not require exactly the same food; but two of the same kind want the same things, and so compete for the same elements. Therefore it is not quite the same condition as happens in nature. When, however, the seedlings were planted in the open ground, there was often very little difference between them, and when transferred from the pots to the open ground, although still in favour of the intercrossed, it was much less so. There are only two alternatives to explain this; either the intercrossed *lost* vigour from being moved, or else the self-fertilised *gained* vigour faster than the intercrossed, and so became nearly equal to them. In Mr. Darwin's book on the "Variation of

Animals and Plants under Domestication," he says that it is necessary to put them under competition, otherwise little or no difference may be seen in the results, showing, therefore, that, apart from the competition, there is not so much benefit to the intercrossed over the self-fertilised as might be expected. 12. Naturalised abroad, self-fertilised plants often gain great vigour, and are the fittest to survive in the struggle for life. I have noted down all the British plants from a number of different lists of floras of foreign countries, to see what was the distribution of our own wild flowers over the world; and what at once struck me as peculiar was that they are, for the most part, the inconspicuous and self-fertilising flowers. Thus *Cardamine hirsuta* is a good example. You probably know *C. pratensis*, the "cuckoo flower" of our meadows. While this is solely European, *C. hirsuta* is found in many countries scattered over the world. *Stellaria media*, the chickweed, is found in a great many places, but *Stellaria Holostea*, the common stitchwort, which is large flowered and requires insects, is nowhere to be found out of Europe. No other species of *Malva* except *M. rotundifolia* is widely dispersed: with the sole exception of *M. sylvestris*, which is in Japan. There is no reason why the conspicuous-flowered plants should not have become dispersed as well as the others. Again, *Solanum nigrum*, the little white flowering night-shade, is found dispersed, while *Solanum Dulcamara* is nowhere seen but here. *Polygonum aviculare*, which bears little inconspicuous green flowers, and is self-fertilising, is found in Australia and elsewhere; but the large purple one, *P. Bistorta*, is only met with here. Moreover the former, a small weed in this country, in New Zealand is completely ousting the native flowers. It is described as being four feet long, and with roots of several feet in length. Now if such is the case, what are we to infer? That there is no appreciable reason why the conspicuous and insect-requiring plants should not travel about as much as the inconspicuous ones; but that if they did, and have disappeared, it is because no insects visited them. Inasmuch as insects, as a rule, keep to particular flowers, and the native insects in foreign countries would continue to visit their own flowers, and would not take the trouble to go to the newly-imported individuals, I infer that, whenever conspicuous forms requiring insect agency have migrated, they have generally perished—in other words, that the self-fertilising are the fittest to survive in the struggle for life.