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and *Cardamine asarifolia* (several plants along the course of the stream); and in the woods, *Epipactis latifolia*, *Veratrum*, &c. After a while, where the valley turns rather sharp to the right, we had to ascend by a path through the woods to the left, which leads over into the Lima Valley, about a couple of miles below Boscolungo, and were soon back to our inn again. We drove back early next morning to the Baths of Lucca; for having come to the end of our drying paper we were anxious to lose no time in preserving our specimens.

III.—*On the Fertilisation of the Cereals.* By ALEXANDER STEPHEN WILSON.

The present paper refers to observations and experiments made upon wheat, rye, barley, and oats, during 1873, and corrects one or two mistakes into which the writer had fallen in a previous paper on the subject. (Bot. Soc. Tr. xi. 506.)

1. *Before Fertilisation*.—From the time at which the ears, or part of the ears, of the four European cereals appear above the sheath, till the time of flowering, the styles and the anthers remain in nearly the same position. During this time the filaments are of such length as to place the lower ends of the anthers in contact with the upper part of ovary, while the styles lie embraced by the anthers; the whole being straight and running in the same direction as the axis of the closed pales. (See figs. 1, 3, 5, 7.)

In each of these four cereals the ovary is of a different form; and it may be noticed in passing that the embryo originating in each has well-marked distinctive characteristics. The styles of the oat also differ from those of the wheat, and these again from the styles of the rye and barley. The anthers of wheat, spelt, barley, and oats, nearly resemble each other in length and form. Their upper ends extend nearly half way to the apex of the pales. But in the rye floret the anthers are much longer, and reach very nearly to the termination of the upper pale. The flower cup, or space enclosed by the pales, is smaller and narrower in rye than in the other cereals.

2. *Opening of the Flower*.—“Many authors,” says Darwin (*Origin of Species*, p. 316), “maintain that impreg-

ination [of Wheat] takes place in the closed flower, but I am sure from my own observation, that this is not the case,

1, 3, 5, 7, Oat, Wheat, Rye, and Barley florets, before fertilisation; 2, 4, 6, 8, the same after fertilisation; *d*, point where spontaneous discharge takes place. Scale, four times natural size. A. S. W., del.

at least with those varieties to which I have attended." We shall see that Darwin and the authors he alludes to are easily reconciled. When we speak of the opening of a flower, we usually mean the obvious distension of the corolla, and the exposure of the anthers and pistil. But in regard to the cereal and other grass flowers, opening is of various degrees. It usually begins about the middle of the spike in wheat, rye, and barley, and at the top of the panicle in oats, while a week or ten days may frequently elapse between the flowering of one part and another.

With what is called the Italian form of two-rowed barley (which is probably the Achillean barley of some of the ancient writers), all the opening necessary for fertilisation, and all that ever takes place, consists in such a mere effort at opening as distends the pales sufficiently to enable the anthers to be pushed up the sides of the flower-cup. If a floret is held up between the eye and the light before fertilisation has taken place, the anthers will be seen through the pales lying in their original position, and if the flower is then opened and inspected, it will be found that the anthers are still unopened, and still retain their bright yellow colour. But if, on looking through the semi-transparent pales, the anthers are seen in the upper part of the cup, fertilisation has taken place; and if the floret is opened the anthers will be found open, with the pollen scattered about on the feathers and inner surfaces of the pales, and the bright colour of the anthers passing away. The inner pale in this form of barley is so tightly embraced by the overlapping edges of the outer pale as prevents further opening. The intra-paleal space, however, is sufficiently large to permit of the pollen grains falling down from the discharging slits upon the styles; for the barley in question maintains an upright ear even when ripe.

In other forms of two-rowed and six-rowed barley, all degrees of opening are common, from a mere inflation of the pales to such complete opening as permits the anthers to be pushed partially or wholly out of the cup. But it frequently happens, even in florets which have fully opened, that all the anthers have not been thrown out; they have simply been pushed up to the edge of the pales, and these coming together again have enclosed them, as if the floret

had not opened at all. This fact must be kept in view by any one who, opening the pales after fertilisation, and finding the anthers still inside, is disposed to contend for the non-opening of such floret. In an ear of Bere (*Hordeum vulgare*) eleven florets on the main rows had thrown out the anthers while three had not; in another, all the florets on the main rows except one had expelled the anthers; in another, all the six rows were opened after fertilisation, and none of the anthers was found enclosed. Delpino contends that opening and non-opening are explained by difference of construction in the florets. There is probably no essential difference in florets of the same rows; but it is quite certain that in some the overlapping of the outer pale is stronger and closer than in others, and that, therefore, the more tightly closed will be least ready fully to open. Observation also proves that the plant is growing more rapidly in one state of the weather than another; and the question presents itself, Has the degree of opening in a given floret any dependence on the current vigour of general growth? None of the rows in the six-rowed varieties seems to have any normal peculiarity in respect of opening; one floret on a row will open fully and fling out its anthers, while another on the same row will retain its anthers till they are pushed out by the ripening fruit.

The different varieties of wheat, so far as known to the writer, observe conditions of opening the flower similar to those of the barleys. Notwithstanding the strength and ultimate rigidity of the pales of spelt, they open even more fully than those of the ordinary wheats. In samples of spelt from Germany, procured by the writer, none of the third florets of the spikelet are fertilised, while in the plants grown by him from these seed many of the third florets are fertile. Many wheat florets never open so far as to give room for the egress of the anthers, some open so far as to allow one or more anthers to get half out, in which position they are caught and held by the reclosing of the pales. In many the anthers are wholly retained, but the general rule is for the floret to open so far as to throw out the anthers.

The rye floret is much longer in proportion to its breadth than the floret of wheat, barley, or oats. The anthers

occupy almost the whole length, and the whole enclosed space above the ovary. In order, therefore, to fertilisation it is an absolute necessity that the rye floret shall fully open. This is also the case in wheat-grass (*Triticum repens*), and other grasses, in which the anthers are nearly continuous with the pales. Cases sometimes occur in which the recurved edges of the inner pale so tightly embrace the anther that it cannot be pushed out even when the flower fully opens.

Amongst the oats, very many florets never open their pales so far as to discharge the anthers. In a great number of cases complete opening seems to be prevented in the lower or main floret by the want of sufficient force of separation in its pales, to push aside the secondary floret which it embraces. Another reason why the anthers of oats are so frequently left inside is, that in general the locusta hangs with its apex downwards, so that even when the bracts open wide, the anthers, hanging perpendicularly, are re-enclosed when the flower shuts. But probably there are other causes obstructing full opening; for the lower floret of the fly oat (*Avena sterilis*), although having very stiff pales and closely hugging three or four secondary florets, opens widely in almost all cases. Wide opening is also the general rule with the wild oat (*Avena fatua*). The cultivated oats open, from a slight dilatation of the valves, to a separation at the points of a quarter of an inch. Cases are to be seen in which the anthers of the oat have discharged the necessary part of their pollen almost in their original position, the inference here being that almost no degree of opening has taken place. If a number of florets are opened after fertilisation has occurred, the anthers will be found either absent, or in all sorts of positions corresponding with the degree of opening; they will be found peeping from between the pales, or somewhere betwixt the edges and their original place.

As stated in a previous paper, opening of the cereal flowers takes place at all hours of the day. I have observed that it also takes place in all kinds of weather, wet or dry. I have observed that spelt flowers open in the morning before the sun touched them. I have also seen them open in a dead calm after sunset (9 P.M.), many of

them had opened and closed within an hour previously. I have likewise seen wheat and spelt flowers open during heavy rain, and in dull cloudy weather. Fertilisation seems to take place when the flower is ripe, independently of any particular state of the weather. In respect of all florets which do not open so far as to eject their anthers, the falling of rain or the blowing of the strongest wind is perhaps a matter of indifference. In respect also of all florets which open pendulously, the falling of rain is obviously a matter of indifference. But when we see, as below, that even in upright, fully opening florets, the fertilising discharge takes place inside the cup, the question occurs, Will not a drop of rain carry the pollen grains down towards the ovary and assist fertilisation?

In wheat, barley, oats, rye, wheat-grass, and probably many other grasses, opening of the flower may be induced by handling the ear in a gentle way when the natural time of flowering has nearly arrived. In rye especially this would form a beautiful lecture-room experiment. I have seen eleven rye florets throw out their bright yellow anthers at the same time on one spike, by simply drawing them through the hand: indeed, the mere transfer of a cut bunch of rye culms from the open air into a warm room will instantly bring out a fine display. Barley and wheat flowers also open from the same causes, though not so freely. The force exerted by some of the grass florets in opening is so considerable that when, for instance, the lowermost inner floret of a spikelet of dandel opens, the spikelet is held apart from the rachis by a tension which counterbalances 110 grains.

Whether the sudden opening of grass flowers upon being touched is to be regarded as a kind of irritability, must at present be passed over. Probably the continued growing of the pollen grains keeps the filaments of the anthers quiescent, until these grains becoming mature, the rising sap is dammed back into the filaments. These are then forced into the sudden growth which takes place. The handling of the spike may simply antedate this process, since it may sometimes be brought about before the pollen is matured, when the anthers are pushed up and tumbled out without

rupturing. But in general dehiscence follows artificial opening in the same way as it follows natural.

3. *Fertilisation*.—A knowledge of the fact that flowering may be artificially anticipated gives great facilities for observing the methods of fertilisation. These methods may be seen and studied either in the field or in the house, since the ears will blossom well and readily after being cut from the plant and carried home. Indeed, single florets broken from the axis and placed under the microscope, have still so much life and force left in them as to go through in a mournful way the beautiful process of fertilisation, and the botanist may thus perpetrate a little furtive act of vivisection, painful only to the poetic imagination.

Break off a barley floret from an ear which is just coming into blossom; open the pales gently, and put it under a low magnifying power. Presently a slight tremor takes place. The anthers begin to move upward. The filaments are visibly growing before the eye at the real rate of six inches an hour. The anthers get more and more distended. They are now half way up the unpretending green chalice. Observe the little slit commencing near the apex of the more advanced. Out darts a little spurt of tiny bullets. Presently the next and the next opens. Instantly another and another spurt of tiny bullets are sent dancing from each half-open suture over the enclosing sides of the pales, or down upon the spreading feathers. Now and then a solitary ball bounds out of the opening cavity over the plain in front of it, as if it had relieved the elastic pressure of those contiguous to it. But spontaneous projection ceases, apparently on the relief of the internal pressure, although the slit continues to extend into an elliptical pore. Still the anthers move upward. A point inside the pale catches the foremost end of one while the filament is growing and pushing from behind, and it falls over on the round orifice, tumbling out by mere gravity a little heap of grains. Another falls out between the pales, and discharges its remaining contents in the air. The third gets entangled in an overlap, and its unnecessary treasure remains inside. (Compare figs. 2, 4, 6, 8, with figs. 1, 3, 5, 7.)

But the same phenomena may be observed in the field with an eye-glass. In order that all the processes may be

seen according to the usual method of nature, watch the ears of awny wheat on a calm day until a floret is caught just beginning to separate the point of its awn from the spike. Gently push back the inner pale a little, and the anthers will be seen rapidly moving upward. Generally, by the time their discharging or upper ends have advanced half way up the cavity of the floret, the slits open, and the discharge consequent apparently on the internal pressure of the swollen pollen grains has taken place. The anthers continue to be pushed upward, dropping out a little pollen here and there. But all discharge after the first one or two spurts arises solely from gravity and the downward position of the slits.

As it is a tedious pastime to watch for the natural opening, the opening which is brought about by handling the ear may always be substituted. For while you are examining one floret, others are sure to begin to swell out and give symptoms of opening, so that the essential process may be watched in any number of cases. The opening of an oat flower with a pincers, when near the time of flowering, will bring on the process of fertilisation under the eye, and the same phenomena may be seen as in the case of barley and wheat. Discharge of pollen takes place before the anthers get outside the corolla.

It is thus seen that in those florets of oats, wheat, spelt, and barley, which even fully open, a discharge of pollen takes place before the anthers get outside. Only from three to five minutes elapse from the time when the anthers begin to move until the filaments attain their final length. After extension these filaments are slightly reduced in thickness.

In the case of rye, which is next to be considered, several of the facts are different. As the anthers in the immature position extend almost the whole length of the pales, the least extension of the filaments pushes the upper end of the anthers, where the discharging slit first opens, out of the flower cup altogether. This is also the case in wheat-grass and others. From a single observation, it is probable that the long anther of the feather-grass (*Stipa pennata*) opens first near the lower end. Were this the case in rye, its fertilisation would be better secured than it is. But as

the rye anthers do not open till beyond the flower cup, certain compensations, as compared with the other cereals, come into play. The quantity of pollen in the rye floret is about ten times greater than in that of wheat, barley, or oats; and on its opening the feathers spring out in curves on both sides.

In various wheats and spelts the points of the feathers are frequently thrown outside, where they are sometimes fixed permanently by the reclosing of the valves, and sometimes they are retracted on the closing of the flower. But the rule in wheat, oats, and barley is, not to expose the feathers. Now, are these precautions taken to fertilise the rye floret successful? We shall see that they are not. We shall see that 24 per cent. of the perfect rye florets in a field are never fertilised.

It thus seems to be the case that wheat, barley and oats, whether they fully or but partially open their flowers, are fertilised before the anthers are visible outside. The coming of their anthers outside, or discharging a remnant of pollen in that position is an accidental circumstance of no essential importance; while with rye an exterior discharge is always essential but frequently a failure. The flowers are seldom open above half-an-hour; and seldom are there more than three or four florets open at one time on a spike.

"It is generally believed," says Mr Alfred W. Bennett (*How Flowers are Fertilised, a Lecture*, 1873, p. 11) "though on this point further experiments are still wanting—that our cereal crops, especially wheat, rye, and barley, are fertilised exclusively by the agency of the wind. The flowers are small and uncoloured, without calyx or corolla; the anthers are hung lightly on the end of long slender filaments; the pollen is very fine and powdery; and insects are hardly ever seen to visit them. Favourable weather (fine and sunny, with light breezes, and yet not so strong a wind as to disperse the pollen to too great a distance, so that it will not perform the purpose for which it was designed) at the time when the plants are in flower—i.e., in the early part of June—is therefore of very great importance for the insuring of heavy crops." But we have seen that the rule which applies to wheat, barley, and oats, does

not apply to rye. We have seen also that the wind is entirely unnecessary to the fertilisation of wheat, barley, and oats. The Belgian farmers who trailed ropes over their flowering wheat to insure complete fertilisation, were doing that which the very appearance of the anthers told them in whispers, not yet heard, had already been accomplished. The pollen of these plants, which the winds disperse, is not that which fertilises, but that which is not required for fertilisation. It is manifest that in the Italian barley, the largest fruited of all the varieties, and which never opens its pales, nor disperses any pollen in flowering, cross-fertilisation has never taken place in all the lapse of its existence; while in the case of the other barleys, wheats, and oats, even the florets which do fully open are self-fertilised before space is afforded for the admission of neighbouring pollen.

Then in regard to rye. I counted at one time ten ears taken at random from a field when nearly ripe, and found that they contained 450 fertilisable florets. The defective highest and lowest florets on the spike, and the middle florets, which sometimes are fertile but more frequently barren, were left out of the enumeration, and only the four rows taken which are usually fertile; of these 107 were barren. Thus, 76 per cent. of the florets were fertile, and 24 per cent. barren. At another time I took from the sheaf fifty ears, and counting in the same way, found 2297 florets, of which 1750 contained kernels, thus giving 76 per cent. of fertile florets, and 24 of barren, as before.

I placed a pot containing several plants of rye and barley in an unoccupied room immediately before flowering. Here consequently they flowered in a dead calm, unaffected by the wind. When the plants were ripe twenty ears of rye were counted as before, and contained 817 fertilisable florets. Of these only 165 had produced kernels. So that in a dead calm only 20 per cent. of rye florets were fertilised. And if 20 per cent. are fertilised by the falling of the pollen from the expelled anthers in a dead calm, while 76 per cent. are fertilised amid the ordinary breezes of the field, 56 per cent. of rye florets are fertilised by the agency of the wind.

Counting ten ears of Chevalier Barley in the open field,

there were 285 florets, of which nine were barren, or a little over 3 per cent. The barley grown in the pot was not well attended to, and ten ears which flowered in the house had only 191 florets, of which ten, or about 5 per cent. were barren. The difference of 2 per cent. I believe to be due to defective watering rather than wind; this comparison not having been thought of till after the plants were ripe. But the fact that the percentage of barley fertilised amid the ordinary motions of the air, and the percentage fertilised in a dead calm are practically the same, proves that the fertilisation of barley does not require the aid of wind, and must therefore result from the intra-paleal discharge; since the extra-paleal discharge in the dead calm falls to the ground, the specific gravity of grass pollen being much greater than that of atmospheric air. It is almost needless to say that one plant of Italian barley of four ears, which also fertilised inside the house, was as fully fertilised as in the field.

Counting the outer rows only of ten ears of various wheats, the percentage of barren florets was 4½.

The main florets of ten ears of Potato Oats in the field numbered 296, of which six florets were barren, or about 2 per cent.

We see, then, that the method of oats, barley, and wheat, more successfully fertilises the ovule than the method of rye. As before hinted, this does not arise from the quantity of pollen being greater in the former than in the latter, but simply because in wheat, barley, and oats dehiscence takes place inside the floret, where, in general, neither wind nor rain can carry away the pollen from the vicinity of the stigma. But barrenness frequently results, not from the non-apposition of pollen, but from defects, or monstrosity. An ear of bere was observed with the flowers on the main rows gaping open, but with the anthers inside shut and destitute of pollen. Emptied anthers speedily get blanched and shrivelled, and, in many grasses, the discharging sutures soon open from end to end. Where anthers are seen hanging outside, straight and yellow, or purple (which they sometimes are), they will be found defective. The stigma is also sometimes defective. An ear of bere was observed, in each floret of which were clustered three ovaries, having two

feathery styles each, while the anthers were merely rudimentary.

4. *Points of Structure.*—A transverse section of a rye anther, a little before puberty, shows four cylinders around the connective, although structurally there are but two lobes. Each cylinder shows about twenty-six grains attached round the interior surface, and leaving the central part of the loculus open from end to end. Making the necessary micro-measurements, each anther of rye is found to contain about 20,000 grains, the three anthers together giving 60,000 grains of pollen for the fertilisation of what is usually considered one embryo, but which, perhaps, may more properly be regarded as a cellular mass, capable of evolving fifty embryos, one of which takes the lead in the ovary, but two others of which may generally be therein detected.

The pollen of three triplets of rye anthers poured into the pan of a delicate balance was found to weigh $\cdot 37$ of a grain. Each floret, therefore, of a fair-sized spike of rye contains $\cdot 123$ of a grain of pollen, and each anther $\cdot 041$ —so that 500,000 ellipsoids of rye pollen are required to make 1 grain weight.

Measuring and weighing the pollen of wheat in the same way a spelt floret was found to contain 6240 grains of pollen, and a spring wheat floret 6864. A set of spelt anthers (which are about the same size as those of the other wheats, barley, and oats), was found to contain a weight of pollen of $\cdot 016$ of a grain. This is only about one-eighth of the weight contained in a set of rye anthers. But the pollen grains of wheat are larger and more spherical than those of rye, so that it takes only 390,000 of these balls to weigh a grain, and while to produce a rye kernel about one-sixth its weight of pollen is required, to produce a wheat kernel only one-fortieth its weight is required. It would be easy further to show that an acre of wheat may produce 50 lb. of pollen, and an acre of rye 2 cwt.; but such calculations are less suited to strict science than to the gratification of popular curiosity.