CORRESPONDENCE.

THE INHERITANCE OF "STRENGTH" IN WHEAT.

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IN a paper "On the Inheritance of Strength in Wheat¹" R. H. Biffen criticises some of the experiments which have been carried out at the Experimental Farm at Ottawa. As his paper contains some inaccuracies and incorrect deductions, a reply seems necessary.

The difference of opinion between Biffen and myself should first be stated. He maintains that strength and weakness (or the absence of strength) in wheat flour form a pair of Mendelian unit characters. My view is that strength is complex: not Mendelian in the ordinary sense of the term, though perhaps depending on a number of Mendelian unit characters working together.

In Bulletin No. 57, of the Experimental Farm series, on "Quality in Wheat" some evidence was brought forward against Biffen's view. He now endeavours to show that this evidence when properly considered really supports his theory. This bulletin he incorrectly refers to as "Report for 1907." The report for that year was not in print at the time Biffen's paper was written.

Before taking up his comments it may not be out of place to call attention to the fact that most of the publications of the Canadian Experimental Farms are designed primarily for the use of farmers and other classes of people of whom very few have been trained as scientists. If therefore some details of purely scientific interest are occasionally omitted, it is scarcely fair for any critic to assume that our experiments are faulty in all unexplained respects. In some cases our publications are less open to adverse comment in this regard than those of other

¹ Journal of Agricultural Science, Vol. 111. p. 86.

experimentalists. For instance, the complete details given in my determinations of the baking strength of flour contrast favourably with the meagre information furnished by some other investigators—so meagre in some instances as to render intelligent criticism of their work quite impossible.

About twenty years ago some crosses were effected at Ottawa between Red Fife and White Fife wheats on the one hand and Ladoga wheat on the other. The Fifes I have shown to be strong wheats, both having practically the same baking strength. Ladoga gives weak flour. Four distinct varieties of wheat of the above parentage (Preston, Stanley, Huron and Percy), after having been grown for about fifteen years and having been selected in the imperfect manner clearly described by Biffen (and being of course entirely unselected so far as baking strength was concerned), were submitted in 1903 to milling experts whose reports, Biffen says, "make it evident that they [these wheats] possess strength of the same order as that of Fife." After some further statements, he says "More conclusive proof of the fact that these varieties once possessed [i.e. in the year 1903] the strength of Fife it would be difficult to find." Biffen has here fallen into the common error of confusing milling tests with baking tests. None of the experts in 1903 made baking tests of the samples submitted to them. One of the experts estimated the strength of the flours by kneading them and then washing out the gluten, a method which has distinct value, though far inferior in accuracy to a baking test and giving sometimes quite misleading results. His conclusions are given on pages 15 and 21 of the Report of the Experimental Farms for 1903. They show that the cross-bred wheats were on the whole distinctly inferior in this respect to the Fifes, though the expert does not clearly state the degree of this inferiority. In the first grade he places two samples of Red Fife and one of White Fife. These are marked "excellent" and "101." In the next grade are put one sample of White Fife and two each of Preston, Stanley and Percy. These are marked "good" and "100." A difference of one point on this expert's very short scale of points for gluten quality is of considerable significance. His tests therefore, so far as they go, prove the essential inequality rather than the equality of these samples. The other experts who examined these wheats at that period made no tests of them equal in importance to those just mentioned. Their opinions therefore in regard to baking strength were, if expressed at all, little better than mere guesses and need no further consideration. I have repeatedly shown that the appearance of wheat is a very untrustworthy guide as to baking strength, although having much to do with the selling price. Surely a "more conclusive proof" of the baking strength of these wheats might be obtained from actual baking trials. This does not seem to have occurred to Biffen and he has also overlooked the interesting fact that some of these wheats, still absolutely unselected so far as baking strength was concerned, were sent to England for the use of the Home Grown Wheat Committee, and after having been grown there were submitted by them to baking tests which showed the cross-bred varieties to be distinctly inferior to Fife wheat grown under similar conditions. By what process of reasoning can this English evidence be brought in line with the belief in the Fife-like strength of these cross-bred wheats?

Having thus reviewed the facts, let us in the light of Mendel's law examine Biffen's argument. He contends that these cross-bred wheats (which had never been selected for baking strength up to that time) possessed the strength of the strong parent in the year 1903, or about the fifteenth generation from the original cross-bred seeds. Anyone who has grasped the significance of Mendel's work will see that this contention is entirely erroneous. It is perfectly clear that if strength and weakness form a pair of unit characters, the unselected fifteenth generation must have consisted of nearly 50 per cent. of strong individuals and nearly 50 per cent. of weak ones, the unfixed (heterozygous) individuals being present only in very small proportions by that time. This is a simple matter of arithmetic and I do not see how Biffen's conclusion can be accepted by anyone when the circumstances are clearly stated. It is fortunate for Biffen that the facts of the case are not as he claims, for, if these wheats had possessed the strength of Fife at that time, the theory of inheritance which he advocates, as well as my own view, would have been upset; since both views call for intermediate baking strength in all unselected wheats of comparatively late generations.

Biffen further assumes that my subsequent selections (non-Mendelian he supposes) were so unfortunate as to give rise to new strains of these wheats in which the Fife-like strength was no longer evident. This assumption is similar to the first and shows again his failure to grasp the significance of his own theory. As a matter of fact, however, these later selections were strictly Mendelian and were clearly explained in the bulletin from which Biffen quotes. I am therefore compelled to save him a second time from the destruction of his own theory. I still consider it disproved, however, by the fact that each of these new selections was obtained by propagation from a single mother plant selected after making chewing tests of many individuals and retaining only those which showed gluten strength as close as could be found to

220

that of Fife. It would be absurd to assume that these strains, so selected, and showing, when propagated, a really remarkable degree of uniformity in all visible respects, all *happened* to be unfixed in regard to baking strength only. This would furthermore involve the assumption that the chewing test, which was advocated and fully explained in Bulletin 57 and which has been adopted by Biffen, is almost or quite worthless. Altogether twelve rigidly selected strains of Fife × Ladoga parentage have been baked and (with perhaps one exception not yet fully studied) none of them has shown baking strength equal to that of Fife grown under the same conditions.

Biffen further says, "we are not told whether Mendelian methods were employed to secure fixity of type." The explanations given in Bulletin 57 and elsewhere are surely clear enough. On page 9 of the bulletin occur these words: "The seed of every plant saved is always sown separately until after it has been found that the characteristics of each particular strain are quite fixed." This is said in explanation of the method of selection followed for the first few years after each cross has been made. In regard to the selection of older sorts, after giving full details as to the chewing tests and explaining their utility as an aid in making rigid selections, the following passage occurs: "By the use of this method, combined with observations on earliness, productiveness, etc. [including of course such obvious considerations as the character of kernels, chaff, awns, heads and straw] the writer has re-selected all the important cross-bred varieties of wheat produced from the crosses made some years ago. These new selected strains have been propagated in every case from selected single plants and show a degree of uniformity which is quite remarkable." Baking tests of the wheat from individual plants in each selected strain (to prove that there is uniformity within the strain) have not been made. They would be extraordinarily difficult. Chewing tests applied in several cases however have not given any reason to suppose that there was any lack of uniformity.

Again Biffen says: "One is forced to the conclusion that the pre-Mendelian methods, so well illustrated in subsequent reports [subsequent to 1903], were considered sufficient for fixing so elusive a feature as strength." This caustic comment is based on extremely slight foundations. My reports subsequent to 1903 contain only two references that I can find to "pre-Mendelian" selection. One of these refers to certain cases where such work was temporarily necessary and the other reference was made chiefly for the purpose of pointing out the weakness of any such methods of selection. The reasons why the work was done in a few instances in a crude manner do not need to be stated in the present discussion; but I may say that these selections were not carried on as a part of my regular work in wheat breeding. Mendel's investigations were well known to me before the year 1903 and all my work since then has been conducted in the light of his valued conclusions.

Biffen closes this part of his paper by quoting four instances to prove that "a number of cases investigated by Saunders would appear to show that strength is inherited in its entirety." Each of the varieties of wheat he refers to was obtained by propagation from a single plant selected from a large number (by the chewing test) and showing unusually high gluten strength. I cannot see what support Biffen's theory obtains from the fact that it is sometimes possible to find a plant of cross-bred origin which possesses strong gluten, especially when, as in the cases of Marquis and Outlook, both parents were strong or very strong wheats.

I do not agree with Biffen that Red Fife is more variable in the baking strength of its individual plants than other varieties. No doubt any wheat which has not been selected for 50 or 100 years could be subdivided into strains of somewhat different baking strength.

It is quite true that Red Fife is usually impure, like other grains, as found in commerce; but at this Farm we keep our seed used for breeding purposes *somewhat* (to say the least) above the commercial standard.

There are sometimes uncertainties in experimental work which even the greatest care cannot altogether overcome, but these defects do not appear to be confined to Canada. A thorough study of Biffen's paper surely justifies the conclusion that his theories are supported in part by observations and deductions which are by no means infallible. The problems connected with the subject of strength in wheat will not be solved until a great deal more work of a patient and thorough character has been done. At present it appears that the absence of strength is due to various causes which may perhaps be roughly grouped under two heads, namely, small quantity of gluten and poor quality of gluten. These two causes (each of which is perhaps complex) seem to operate either together or separately, and it would be very singular if one simple rule of inheritance could be found to govern all cases; and even if we seek to dispose of most kinds of wheat in this easy fashion, in what group shall we place those varieties which are quite deficient in strength for several months after threshing but which, on long keeping, ultimately rise to the very highest rank? Strength is indeed well described as an "elusive feature." Were it a Mendelian unit character it would be quite otherwise.

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By R. H. BIFFEN.

IF, as I gather from the above, Dr Saunders is prepared to jettison the reports of the milling experts and the chemist and the independent report from the Minnesota Station and admit that they are no longer worthy of consideration, the position is to a certain extent simplified. Any attempts to explain the decadence of the strength of the varieties Percy, Preston, etc. between the years 1903 and 1906 then become unnecessary. With this view I am in complete accord, for it agrees with our own baking trials, carried out before the publication of the Canadian tests, which showed that these wheats were distinctly inferior to the Fifes.

It is however only fair to state that my remarks with regard to the possibility of isolating heterozygotes were based on experiments made whilst growing these varieties for the baking tests of the Home Grown Wheat Committee. In a series of single plant cultures grown with the idea of reducing each of the "varieties" to a single type, individuals were found which were heterozygous with regard to chaff colour and to the presence or lack of beards. It is true that none were found producing two forms of endosperm, but in view of the fact that it is apparently impracticable to detect, by inspection, a mixture of Ladoga and Red Fife¹, this cannot be wondered at.

Further, criticisms with regard to the methods of selection were, I think, called for. The statements quoted by Saunders in the 1907 Bulletin are certainly explicit enough. In the original however the sentence preceding his quotation runs, "for the last few years the method of selection by single plants only has been used²." The qualification "few" becomes of importance when one takes into consideration the facts that these baking trials were carried out on the crops of the years 1905 and 1906, and that a sufficient bulk of grain for reliable tests and duplicates is not readily obtained in one season from a single plant. The abandonment of the old policy of mass selection and its

¹ Saunders, Evidence before the Select Standing Committee on Agriculture, etc., 1905, p. 220.

² Saunders, Bulletin No. 57, 1907, p. 9. Owing to an error in transcription this Bulletin was incorrectly described as a Report in my previous paper.

replacement by a more scientific method is an event of great importance in the history of these experiments. If I translate "few" correctly it should have occurred about 1904, or even 1903, yet references to the Reports for these years, though they show ample evidence of the necessity of the change in the case of such "varieties" as Early Riga and its component varieties Downy Riga and Riga, are far from explicit. In the case of the varieties in question the only information I have been able to find is that they "were subjected to a very careful reselection, sufficient seed being obtained in each case to sow the fortieth acre plot¹."

Although Saunders has simplified the problem by showing that the previous reports on the strength of these varieties may be ignored, he still fails to bring forward further evidence to show that his determinations of the baking value of the varieties Percy, Preston, etc. justify the view that the inheritance of strength is on non-Mendelian lines. The mere statement that the Fifes are strong wheats and Ladoga is weak is of little value to the plant breeder. No one will question the fact that the Fifes, in the mass, are strong, and equally so no one with any experience of them will assume that individual plants are fair representatives of the mass, since both Red and White Fife are known to be mixtures of many types. I refrain from quoting my own experience with these varieties, for abundant evidence of the fact is provided by the "somewhat pure" stocks of the Canadian Experimental Farms. Thus in 1904² we learn that "our White Fife was most carefully hand picked during the winter, and we are sowing it this spring quite free from red kernels"-that in other words the stock was not even true to so obvious a feature as colour. Similarly in the case of Red Fife we find reference after reference³ to the fact that it can be selected into "strains" varying in earliness, productiveness and strength. In one case indeed baking trials have been made with one strain showing a strength greater than the average, the existence of which indicates the existence of strains of under average strength. Yet this mixture is one of those used as material for critical experiments. Under the circumstances one cannot wonder that no answer is forthcoming to the question, "How does the strength of Percy, Preston and Huron compare with that of the parent plants ?" Nevertheless it must be given before any conclusions can be drawn from the baking trials described in the 1907 Bulletin.

- ¹ Central Experimental Farms, Report for 1904, p. 258.
- ² C. E. Saunders, Evidence before Standing Committee on Agriculture. etc., 1904, p. 142.
- ³ Ibid. 1905, p. 218.