

THE SUPPRESSION OF CHARACTERS ON CROSSING.

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THE publication in a previous issue of this *Journal* of the paper "On the genetics of 'rogues' among culinary peas¹," in which attention is called for the first time to a case in which a group of characters introduced by one of the original parents fails to affect the F_2 generation has led me to place a somewhat similar case on record in spite of the fact that the investigations dealing with it are still far from complete.

The character in this instance is the mouse-grey colour occurring in the glumes of the well-known Rivet wheat (*Triticum turgidum*). In this variety, and indeed in all of the grey-chaffed wheats I have been able to obtain up to the present, greyness is invariably associated with the presence of a quantity of silky hairs on the glumes so that all grey wheats are "rough-chaffed." The converse that all rough-chaffed wheats are grey however is not true, for white and red rough-chaffed varieties are moderately common.

Crosses between red or white rough-chaffed wheats and varieties with glabrous chaff show simple dominance of roughness followed by segregation into rough and smooth in the proportions of three of the former to one of the latter.

Where however roughness is associated with greyness, as for instance where Rivet wheat is used as a parent, the two characters tend to be coupled. In certain crosses with varieties of *Triticum vulgare* the coupling appears to be complete since all of the rough-chaffed forms occurring in the F_2 generation have grey chaff. In such cases the ratio for rough grey to smooth white is as 3 : 1. However none of the F_2 generations have so far exceeded some 300 individuals so that there is the possibility that the expected smooth grey and rough white might occur if still larger numbers were raised. In another cross of the same

¹ W. Bateson and Caroliue Pellow, *Journ. of Genetics*, Vol. v. p. 13.

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nature between Rivet wheat and Red Fife a different state of affairs is met with. The F_2 generation in this case contained black, grey and white-chaffed wheats. Several F_2 's of this parentage have been raised, giving in all some 2000 plants, but the number is inadequate for a complete statistical examination, in view of the fact that a large percentage of the plants are sterile and consequently one cannot obtain much information from the F_3 generations. The most that can be said at present is that there are two classes of blacks, one rough and one smooth, corresponding forms amongst the white-chaffed individuals and no smooth greys.

Crossing the smooth black with rough white, the nearest approach so far possible to introducing one of the dominant characters on either side of the parentage, results in an F_2 generation showing coupling on a 3 : 1 : 1 : 3 basis¹.

Crossing Rivet wheat with Polish wheat (*Triticum polonicum*) gives a totally different result to any of the crosses with *T. vulgare*. This wheat has white glumes which are so slightly hairy that they are generally described as glabrous. The glumes are further characterised by their enormous length which under ordinary conditions is some three times as great as that of any other wheat. The F_1 plants of this parentage, no matter which way the cross is made, have a pale grey chaff. Isabelline white is probably the most accurate description that can be given of the colour. It is not unlike that of the Polish wheat, but a faint grey tinge is present much as there is a tinge of blue in many white-flowered varieties of Campanulas derived from blue species. Thus the full dominance of grey seen in all of the other Rivet crosses is wanting.

The F_2 generations from these crosses differ altogether in their general character from the crosses with the varieties of *T. vulgare*. The latter are characterised by the occurrence of a bewildering, though evidently definite, series of unexpected forms such for instance as plants with bright grass green instead of glaucous foliage, with ears of the spelta type, with branching ears, dwarfs, etc. The former show no such features but merely individuals with the short or long glumes of the parents and a series of plants with an intermediate glume length. The short and the intermediate glumes are all markedly rough whilst the long-glumed forms are practically glabrous. Throughout the whole series containing over 2000 plants raised from 20 separate F_1 's the glume colour was identical with that of the Polish wheat. In the

¹ Engledow, *Proc. Camb. Phil. Soc.*

following season 500 cultures, containing from 50 to 100 plants each, were raised from individuals of the F_2 generation and since then a few of the homozygous forms have been carried on to the F_4 stage. No counts of these later generations have been made but it is safe to say that the whole series of plants contained at least 100,000 individuals. Without exception the chaff colour was that of the Polish wheat. The number of plants dealt with appears to be sufficiently large to warrant the statement that in this case the grey chaff character has been totally suppressed.

One or two other coloured forms have recently been crossed with Polish wheat in the hope of finding similar cases but without success. Various red-chaffed wheats have given red F_1 plants and a normal segregation of three red to one white in the following generation whilst a smooth black wheat (from Rivet \times Red Fife) has given a blackish F_1 , segregating into blacks and white in the F_2 . It promises to be of some interest however, for the colouring is confined to the plants with short or intermediate glumes. Further crosses made with homozygous forms of what may fairly be described as "alba" forms of Rivet wheat, from the cross Rivet \times Polish, have merely behaved as ordinary white rough-chaffed wheats when crossed with smooth white varieties.

The suppression of the grey character occurring in Rivet wheat bears an obvious resemblance to the suppression of the type characters when the rogues of culinary peas are crossed with the type plants. There are however differences which may have some significance. The F_1 of rogue crossed by type or type by rogue shows clear signs of the type in the early stages of growth, though these gradually disappear and the plant becomes rogue-like and in future generations throws rogues only. In the case of the wheat no signs of the grey character can be detected at early stages of growth since this feature only develops at the stage in which the grains of the plants are practically mature. Further the colouring appears to be independent of any other features which can be recognised in the early stages of growth. In the peas there is other evidence pointing to the fact that the type characters are left behind in the base of the plant and consequently cut out of the germ lineage¹. But in wheat there is no great difference either in the position or the date at which branches are formed. All of the branches are basal, arising at ground level from nodes so closely clustered together that they are almost unrecognisable. At first sight then similar phenomena can hardly be looked for. Yet it is possible they exist for

¹ Bateson and Pellow, *Proc. Roy. Soc. Ser. B*, Vol. LXXXIX. p. 174.

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a solitary case has been met with where a rough grey wheat crossed with a smooth white has given F_1 plants bearing rough dark grey and rough white ears. The plants were well developed and thoroughly matured so that there can be no question of the genuineness of the phenomenon. The F_2 generation of this cross still has to be raised, and until this has been examined there must be some doubt as to whether similar phenomena are being dealt with.

In wheats it is possible that the suppression of characters is more general than it appears to be at present. A considerable number of examples are known where recessives make their appearance in F_2 generations from crosses of parents showing dominant characters only. Thus red-grained varieties crossed together frequently produce white-grained forms even though the parents breed perfectly true to their red colour. In the commonest cases the ratio of red to white is as 15 : 1. The ratio has been thoroughly established by Howard¹. Nilsson-Ehle², who first called attention to the fact, has suggested that it is due to there being various red-producing factors C , C_1 , C_2 , etc. The parent wheats then have a constitution represented by Cc_1 and C_1c and the gametes of the hybrid form four classes CC_1 , Cc_1 , C_1c , cc_1 . The combination of cc_1 with cc_1 will thus occur on the average once in sixteen times. Similarly by assuming the existence of three distinct red-producing factors, a ratio of one white to 63 red can be accounted for. Such proportions probably occur from time to time, but a wholly satisfactory demonstration of their existence has not been given up to the present.

On this hypothesis the highest frequency with which white can occur in such crosses is one in 16. But the ratio of one in four has recently been found in such a cross between Squarehead's Master and a deep red wheat collected in the western provinces of China and at present unidentified. The same cross and another between Squarehead's Master and a corresponding white form of this Chinese wheat has given bearded plants in the F_2 generation though both parents are beardless. The proportions are again approximately one bearded plant to three beardless.

It is possible that these cases represent terms in a series beginning with complete suppression of a dominant character, then its suppression once in 4 times, once in 16, once in 64, and so on, but it is difficult to devise methods for testing the hypothesis.

¹ Howard, *Mem. Dept. Agr. in India* (Botanical Series), Vol. v. p. 1, 1912.

² Nilsson-Ehle, *Kreuzungsuntersuchungen an Hafer und Weizen*, 1909, p. 68.