THE INHERITANCE OF GLUME LENGTH IN *TRITICUM POLONICUM.*

A CASE OF ZYGOTIC INHIBITION.

By W. O. BACKHOUSE,
Economic Botanist to the Argentine Government.

(With Chart.)

THE sub-species of *Triticum* known as *T. polonicum* is characterised by long glumes which, in extreme cases, can attain a length of 40 mm. whereas that of an ordinary wheat is in the neighbourhood of 10 mm. only. There is a large number of varieties of *T. polonicum* known, varying considerably in minor characters such as colour of leaf, colour and shape of grain, degree of felting, etc., also in glume length itself, some having an average length of about 19 mm., others as high as 28 mm. The sub-species *T. polonicum* hybridises easily with both *T. durum* and *turgidum* and shows[1], by the total lack of sterile individuals in F_2 when crossed with varieties of the former, that it might be considered, genetically speaking, merely an aberrant form of the sub-species *T. durum*. The result of hybridising the long and the short glume lengths is a first generation intermediate in this respect, splitting in the second into long, intermediate and short in the ordinary 1 : 2 : 1 ratio, but not in a manner possible to classify by eye and necessitating the plotting of a curve to show the segregation.

When at Verrières, in 1911, through the kindness of M. Ph. de Vilmorin, the writer was able to examine a collection of varieties of *T. polonicum* grown there and was struck by the fact that there were none with perfectly smooth glumes and, furthermore, that the shorter the glume of the variety, the more felted did it seem to be. The longest glumed varieties, being only faintly pubescent, would roughly speaking

[1] R. H. Biffen, *Journal of Genetics*, Vol. v. p. 225.

be classed as smooth. With the object of investigating this, in 1912 a cross was made between a variety of *T. polonicum*, with an average glume length of 29 mm. and very faintly pubescent, and a variety of *T. durum*, which will be referred to in this paper as *Kubanka*. This last is a smooth and otherwise typical example of *T. durum*, with an average glume length of 12 mm. The first generation was a hybrid of intermediate length—actually of an average of 18 or 19 mm. It was, however, remarkable in that it was distinctly pubescent—very much more so than the *polonicum* parent. The second generation was surprising, for it was soon observed that there was a proportion of plants bearing fully pubescent ears—pubescence, be it remembered, is a dominant character—yet the variety of Polish wheat used as a parent would have been classed as smooth in comparison with such a wheat as Rivet or Essex Rough Chaff.

At harvest time, a middle glume in the ear of each plant was measured and a curve plotted of the number of plants of each glume length in millimetres (Chart[1], Fig. 1 a). The plants were also classified into pubescent, intermediate and smooth, by means of a hand lens. The *polonicum* parent would have fallen among the intermediates in this classification, while the smooths were, as far as could be seen, perfectly glabrous. The numbers observed, considering glume length alone, were as follows:

	Long and Intermediate	Short
	172	55
Expectation ...	*170·25*	*56·75*

A glance at the curve of this family will show that there is no dividing line between the longs and the intermediates but, actually, the shorts can be distinguished by eye—that is to say, an extra short glumed heterozygote. A starved plant, for example, which might fall in the 14 or 15 mm. lengths class, has an indefinable something about it which points to its really belonging to the heterozygote class.

The carrying of large numbers of plants into the F_3 generation showed that, while only two mistakes were made at the short end of the curves, it had been impossible to pick out any but the extreme longs with the certainty that they would be pure to their particular length. Considering those with a glume length varying between 10 and 14 mm. as being pure short segregates and those between 15 and 31 mm. as including both the longs and the heterozygotes, a count of the proportion of pubescent individuals shows that in the short glumed

[1] See pp. 130, 131 and explanation on p. 133.

class, the roughs predominate in the ordinary 3 : 1 proportion (Chart, Fig. 1 b).

	Felted Glume	Smooth
	40	15
Expectation ...	*41·25*	*13·75*

Examining 56 individuals, the theoretical expectation of homozygous longs, and beginning at the extreme long end of the curve, it was found that there were, among them, no individuals which could be called felted, though with a lens a short velvety pubescence was seen on most. Among the individuals with glume length between 15 mm. and 22 mm., which may roughly be said to comprise the heterozygotes, the proportion was 85 felted to 31 smooth; but here there were only 15 individuals which could confidently be called felted—in the majority of cases the closest scrutiny was needed to determine to which category they belonged.

Finally the long class were examined critically—with the help of a lens and the individuals selected which appeared to be absolutely smooth —as smooth as the original short glumed *Kubanka*. These plants were grown the succeeding year and found to be all pure longs except two, and, what is more important, a careful inspection with a lens showed them to be also breeding true to this smoothness; a smoothness which, however, turned out to be only apparent in some cases.

Test crosses were made between these smooth lines and the original *Kubanka*, also other *durums*, to see whether the presence of the pubescence in any way affected the segregation of glume length. The second generations from these test crosses were surprising for, while some were all smooth, others behaved in the same way as the original cross (giving a 3 to 1 proportion of roughs and smooths among the short glumed class), differing only in that the pubescence was of a minor degree, as exemplified in the Canadian variety *Prelude*. From this it will be seen that the long glume was able to inhibit the expression of a dominant character and, furthermore, that there was a direct relation between the length of the glume and the degree of felting—the greater the glume length, the less being the pubescence, even among the variable heterozygotes. This will be better illustrated in the following case.

The same variety of *T. polonicum* used in the first experiment was crossed with a felted, black glumed variety of *T. turgidum*, not unlike Rivet wheat of which it is, in fact, a descendant. The average glume length of the *turgidum* is 11 mm. and of the *polonicum* 28 or 29 mm. The first generation was intermediate in glume length—varying between 14 mm. and 17 mm. It was fairly felted and in colour white or faintly

tinged. In this experiment the *polonicum* will be considered smooth, as indeed it is in comparison with the other; the classification was done by eye, unaided by a lens. The second generation was plotted as a curve (Chart, Figs. 2, 3, 4 and 5) in the same way as the Kubanka Polish cross. Here again it was impossible to separate the pure longs from the heterozygotes and statistically there is no sharp dividing line between the shorts and the heterozygotes (Chart, Fig. 5). However it is fairly safe to say that the pure shorts are comprised among those with a glume length between 9 and 13 mm.—though undoubtedly several of 13 mm. are poorly grown heterozygotes.

The ratio of short glume to long is:

	Long and Intermediate	Short
	514	178
Expectation ...	*519*	*173*

There were 692 plants in this family, besides 39 which were not noted, being too green at the time of harvesting to determine the colour.

The second curve (Chart, Fig. 4) shows the total analysed into those individuals which were felted like the short glumed parent and those (shown by the dotted line) which were practically smooth, like the Polish parent. Here again, it will be seen, the length of the glume has acted as an inhibitor of pubescence. A study of the colour shows this inhibiting nature even more clearly (Chart, Figs. 2 and 3). With the single exception of one plant of 16 mm. glume length, *all* the fully coloured individuals are between 8 and 13 mm.—among the shorts, in fact. The proportion is:

	Tinged and White	Coloured
	129	49
Expectation ...	*133·5*	*44·5*

It was impossible to draw a really satisfactory distinction between the heterozygous tinged or faintly coloured, and the colourless, as the faintly tinged individuals were easily confused with stained whites, but the pure blacks were easily classified. Nevertheless Chart, Fig. 3, shows a curve of those individuals which were considered to be tinged.

The point of interest which attaches to this curve is the distribution of the tinged individuals; it will be seen (Fig. 3) that they are not quite evenly distributed among those with glume length varying between 13 and 20 mm., but that they occur with greater frequency at the short end of the heterozygote curve. The colour seemed to be quite independent of the pubescence. To ascertain whether, among the

longs, there existed some which, though they could not show it, were, in fact, homozygous for colour, five long glumed individuals were crossed with the short glumed *Kubanka* and the first generation plants grown this year (1916). There is no need to wait for the second generation for the results. Two individuals gave all tinged, one gave all white, and two gave a mixture of tinged and whites. There can be no doubt, therefore, that when the second generation is grown and true shorts appear, there will also appear fully coloured individuals.

Only two famiiies of long × short have been described but they are typical of no less than seven second generations grown, all of which show that the long glume in wheat behaves as an inhibitor which, in extreme cases, is as complete as though it were a case of genetic repulsion. There remains only one thing more to note—that from such long and short glumed crosses it is possible to isolate a number of pure lines, each with a different average length and breeding perfectly true to its particular length.

It is possible that the greater variation in length of glume among the *polonicums* is merely due to the effect of magnified small differences, these escaping observation in the ordinary short glumed wheats. If a curve be plotted of the variation in short glumed wheats, this is always steep and acute; long glumed varieties, on the other hand, however often reduced to single plant cultures and so purified, always give a long low curve. The heterozygote curve is more or less intermediate in shape between the two parents[1].

Should it be the case that the apparent greater variation in glume length is only due to a magnifying effect of the extra long glume, then it seems possible to regard *T. polonicum*, which has always been considered a good sub-species in wheat, as merely a number of variations of *T. durum*, differing from the short glumed type in one single unit character which makes the long glume. Thus, had the existence of black and fully pubescent *polonicums* been possible, a separate sub-species would possibly never have been created.

Further experiments with *T. polonicum* throw some light on the strange behaviour of Polish Rivet crosses[2].

I have been able to examine some of Professor R. H. Biffen's material and am familiar with the behaviour of this cross in England. When leaving for this country, I took with me, in the form of grain, hybrids

[1] R. H. Biffen, *Journal of Agricultural Science*, Vol. I. Part 1.

[2] "Suppression of Characters on Crossing," R. H. Biffen, *Journal of Genetics*, Vol. v. Part 4.

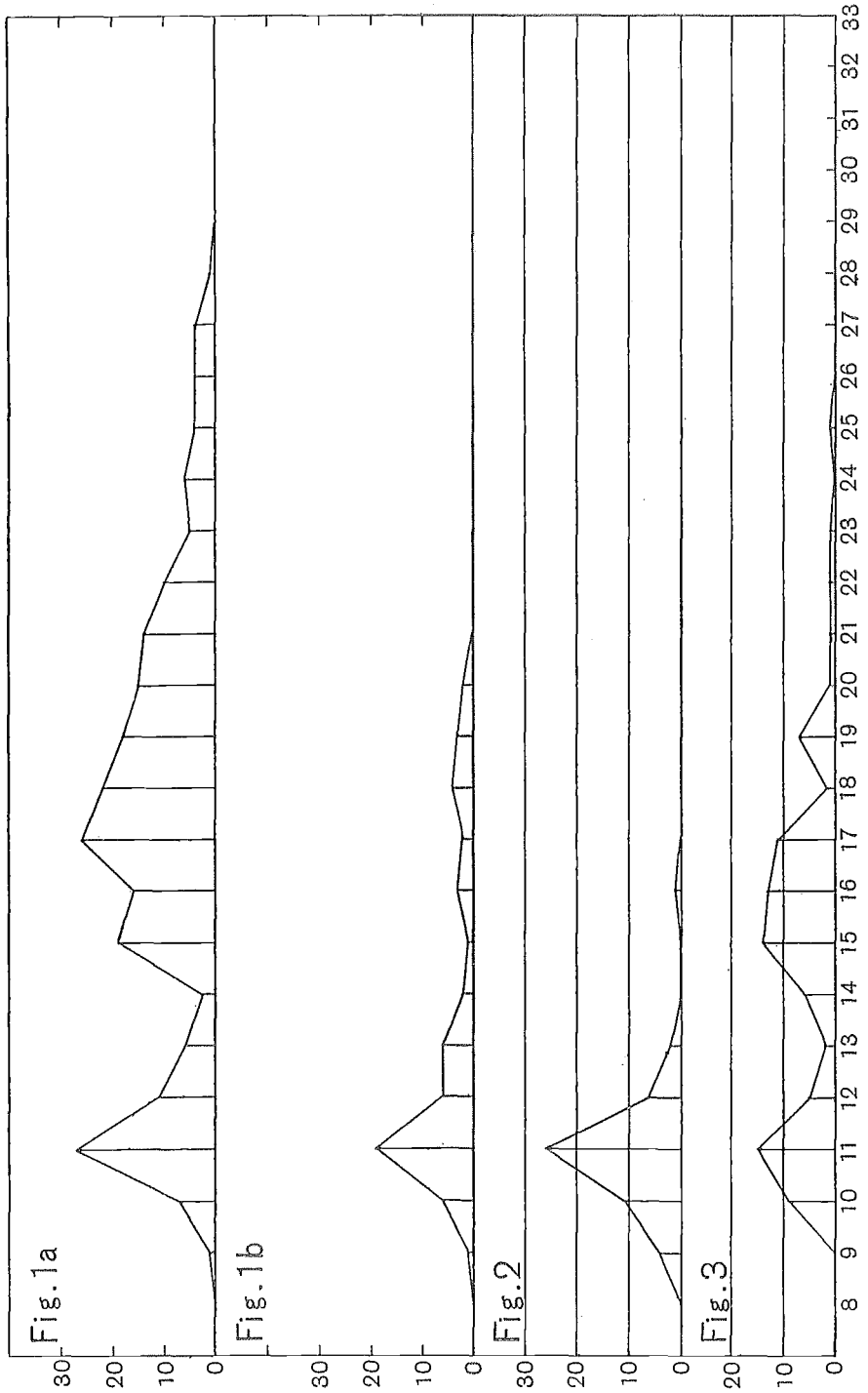
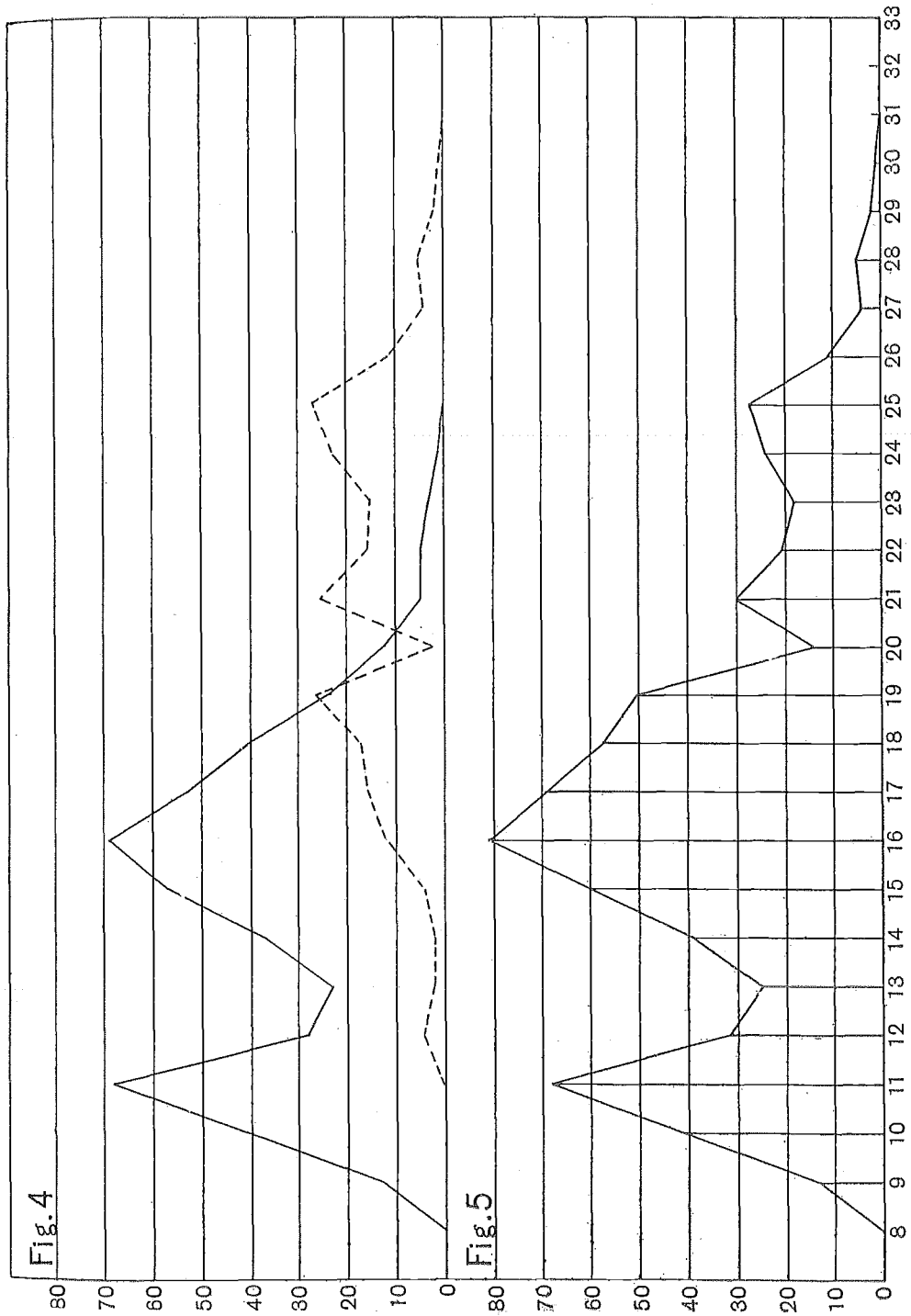


Fig.1a
Fig.1b
Fig.2
Fig.3
0
10
20
30
8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33



For explanation see p. 133.

already made with the same strains of Rivet and of Polish wheats as used by Biffen. The first generation was grown at Pergamino, in 1913, and was notable from the start as being decidedly tinged. The second generation was divided and grown, in 1914, in three different places, viz. in the north, centre and south of the wheat producing area of the Argentine Republic. In the north, all the individuals were colourless, as in England. In the centre, at the latitude of Buenos Aires, some of the short glumed individuals were tinged. In the south, in the Pampa, the coloured ones were fairly clearly defined and could be classified, giving the following proportions:

Rivet × *Polish* F_2. *Guatraché, Pampa.*

Long and Intermediate glume length		Short glume length	
72		30	
Coloured	White	Coloured	White
0	72	7	23

Three doubtful shorts grown in 1915, to test, bred true to short glume, but not to colour, and gave a total of 7 white to 13 coloured. The proportion is peculiar but it is always difficult to distinguish the homozygous coloured individuals from the heterozygous tinged ones.

Polish × *Rivet* F_2. (*Reciprocal of the other cross.*)

Long and Intermediate glume length		Short glume length	
25		9	
Coloured	White	Coloured	White
0	25	4	5

It will be observed that here again the coloured individuals are only found among the short glumed category. The coloured segregates of these crosses are never quite so deeply coloured as Pedigree Rivet wheat itself and grade almost imperceptibly from coloured to tinged and tinged to colourless.

The interest of the experiment, however, lies in the fact that, whereas in England the colour disappears and does not return in any subsequent generation, the result of growing F_2s, obtained in identically the same way, in the Argentine, is to prove that at any rate the colour is there and, given suitable climatic conditions, will show itself. Rivet wheat, grown for comparison, had the same peculiar mouse-grey colour as in England and was no darker in this climate.

The cause of the suppression of colour in this particular cross must be sought for in the shape of an inhibitor, brought in, either by Polish wheat and meeting something in Rivet to release it, as it were, or *vice versa*; for this particular strain of *polonicum* crossed with coloured varieties other than Rivet gives coloured descendants, in climatic conditions under which, crossed with Rivet, they are colourless.

EXPLANATION OF CHART (on pp. 130, 131).

Fig. 1a. Family 74/14. *Kubanka* × *Polonicum*.

Curve of glume length plotted for 227 individuals, showing that, whereas the short glumed individuals, namely those whose glume length varies between 9 and 14 mm., are easily distinguished from the rest, there is no discontinuity in the curve between the heterozygotes (of, say 15 mm. to 22 mm.) and the bulk of the homozygous longs.

Fig. 1b. Curve of those individuals which were completely felted. It will be seen that there are few of heterozygote glume length and no longs.

Fig. 2. Family 104/16. *Polonicum* × *Turgidum* 179.

The fully coloured individuals. These, with one single exception, are among the short glumed plants.

Fig. 3. Those individuals which were not fully coloured and classed as tinged. Owing to gradation in colour from plainly tinged to faintly tinged or stained white, this curve is only of relative value, but serves to show that among the real longs there were only three or four with a trace of colour.

Fig. 4. The same curve as in Fig. 5, resolved into felted individuals—shown by the whole line—and those classified, without the aid of a hand lens, as smooth—shown by the dotted line.

Fig. 5. Curve of the whole family of 692 plants, plotted for glume length alone.