

INHERITANCE IN BARLEY.

I. THE LATERAL FLORETS AND THE RACHILLA.

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(With 3 Text-figures.)

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INTRODUCTION.

THIS account of the inheritance of certain of the characters of barley is to be regarded as provisional. It represents the results of observations made from time to time upon F_2 's which have been raised for plant breeding purposes.

The "lateral floret" has become a familiar problem in barley genetics. It is believed that although the general solution of this problem has been reached, there still remain a number of interesting side issues which can be decided only by raising large and complete F_2 's and by a histological study of the various degrees of development of the floret.

That the artificially produced variety *H. inermis* (obtained by Rimpau from the cross *H. Steudelii* \times *H. trifurcatum*) offers a complete solution to the problems of the inheritance of awn and lateral floret seems certain; but *H. inermis* fluctuates very readily under environmental change and for this reason the evidence obtained so far from its crosses has not been used in this paper. A study of the seasonal fluctuation of *H. inermis* and of the two "intermediums" (*H. Hustoni* and *H. transiens*) is, as crosses have repeatedly demonstrated, essential to finality in the elucidation of the awn and lateral floret problems.

I. THE RACHILLA.

In the barleys two forms of rachilla are recognised. The first [(a) in Fig. 1] has long, stiff, pointed hairs which are inclined to the axis of the rachilla at a small but variable angle. The appearance of such a rachilla is suggestive of a diminutive ear of barley, the rachilla hairs corresponding to the awns of the ear.

The second type of rachilla [(b) in Fig. 1] has a longer and more cylindrical axis, and the hairs upon this axis are all short, fine, slightly curled, and woolly in appearance. Commonly this type is known as the "smooth" rachilla, the first type being called the "bristly" rachilla.



Fig. 1.

Atterberg (1) uses rachilla character in his classification of the Barleys to separate the "distichum" group into sub-groups, and in connection with it he further employs a somewhat obscure and variable character, viz. the prickles or projections on the nerves or veins of the outer palea [the "zähnen" of Körnicke (2)]. In the experimental results here recorded, these "projections" do not appear as a "character," for their variability renders sorting unreliable.

At first both the hairs (or bristles) and the axis of the rachilla were noted in all the F_1 and F_2 plants, but it became apparent that in certain cases referred to later the axis was liable to considerable and unaccount-

able fluctuation, and consequently inheritance results are recorded for hairs (or bristles) only.

In all cases observation was confined to the median florets, for these florets alone exhibit well-developed rachillae throughout all the different botanical classes of the barleys. The rachilla of the lateral floret reaches a stage of development which corresponds very closely with the general development of the floret itself. Thus in *H. hexastichum* the rachilla of the lateral is as well developed as that of the median. The "inter-medium" barleys (*H. Haxtoni* and *H. transiens*) have full "bristly" rachillae on their medians, while the rachillae of the laterals are long and slender in the axis, the bristles being short and fine. In the "distichum" barleys the laterals are small and infertile, and, whether the rachillae of the medians be bristly or smooth, those of the laterals have hairs which are so diminutive that they are scarcely visible even under the microscope. Finally, in the "decipiens" barleys the lateral floret is reduced to two very small empty palcae and no trace of rachilla is to be seen.

Certain varieties of barley show very great fluctuation in the form of rachilla. In *Praecox* (*H. hexastichum*) in particular, a certain proportion of abnormal rachillae is always found. It not infrequently happens that only one rachilla on the whole ear is abnormal. Fig. 2 (*a*), (*b*), (*c*), (*d*), (*e*), (*f*) illustrates commonly occurring abnormal types in this variety. The normal type is the "bristly" (see (*a*) in Fig. 1).

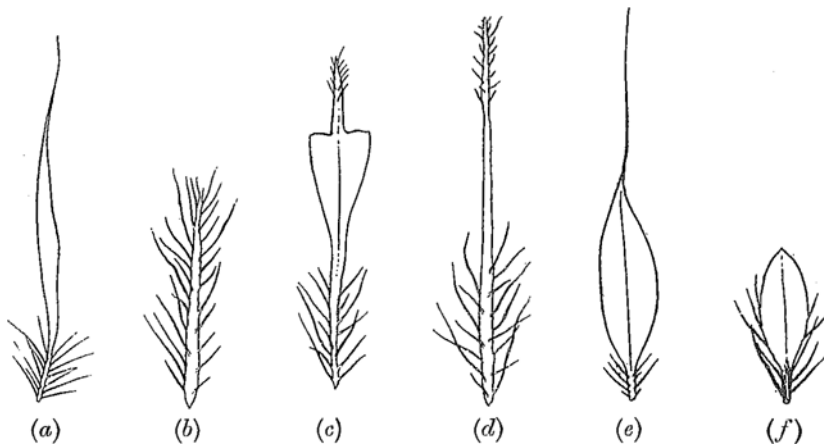


Fig. 2.

Some of the abnormalities present a "leaf-like" form and in the F_2 of a *Praecox* × *Archer* cross there occurred the type shown in Fig. 3,

in which the rachilla bore two "paleae." These paleae contained no traces of reproductive organs.



Fig. 3.

There are a few hairs on almost all parts of the barley plant. In the following regions hairs are abundant in varieties in general:

- (i) Rachilla.
- (ii) Glumes.
- (iii) Awns (short, strong, spikes).
- (iv) The thin edges of the rachilla segments.
- (v) The lodicules (in the form of a fimbriation).
- (vi) Roots (root hairs and therefore not strictly analogous to glume, etc. hairs).

A comparison between Archer and Chevallier barleys for example shows that the difference in the hairs of the rachillae exists, though it is not so marked, in (ii), (iii), (iv), and (v). In the root hairs (vi), no constant difference appears to exist. Thus it is suggested that one factor governs the type of hair in all the regions (i)—(v). Examination of a considerable number of barleys supported this view, but (iii) had finally to be removed from the list on account of the evidence of the "distichum" barley *H. d. persicum*. This sub-variety has smooth awns but both rachillae and glumes bear long bristly hairs. It is of interest to note that another well-known smooth-awned barley, *H. d. glabrum*, has smooth glumes, extremely short lodicule processes, and rachilla hairs which are far shorter and finer than those of Chevallier.

It is desirable to study this "parallel" development of the hairs of different regions and, in particular, to investigate the root hairs, for upon

them may depend some of the most important components of "yield." Investigations to this end are being undertaken. [The comparative morphology of the "hairs" on different parts of the plant may, perhaps, afford indications as to localities in which "parallel" development is to be expected.]

The undermentioned crosses supply data concerning the inheritance of type of rachilla.

Cross No. 53.

Russian Goldthorpe, No. 9 \times Plumage

2-row { } 2-row
Bristly { } Smooth

F_1 = four plants; all bristly

F_2 = 188 plants. Bristly : Smooth = 144 : 44
= 76.6% : 23.4%

In this case the deviation from 3:1 expectation is less than half the standard error.

Cross No. 32.

Russian Chevallier, No. 7 \times Inerme

2-row { } 2-row
Smooth { } Bristly

F_1 = 2 plants; both bristly

[The seeds of these plants were sown on separately and the F_2 families were designated 32/1 and 32/2.]

F_2	32/1 = 299 plants.	Bristly : Smooth = 220 : 79
	32/2 = 194 plants.	Bristly : Smooth = 149 : 45
F_2	Total = 493	Bristly : Smooth = 369 : 124
	i.e. Bristly : Smooth = 74.8% : 25.2%	

In this case the deviation from the 3 : 1 expectation is far less than the standard error.

Cross No. 57.

Praecox \times Plumage

6-row { } 2-row
Bristly { } Smooth

F_1 = 3 plants; all bristly

F_2 = 186 plants. Bristly : Smooth = 146 : 40

This suggests, but is by no means closely in accordance with a 3 : 1 ratio. Observation and theory compare thus :

		Bristly	: Smooth
Observed	78.5 %	: 21.5 %
Calculated (3 : 1) ...		76 %	: 25 %

The deviation is thus about four times the standard error and cannot, therefore, with assurance, be regarded as a fluctuation of sampling.

The abnormal rachilla forms found in the Praecox parent (see above) made their appearance in F_2 . They were not confined to any particular type or types of F_2 (as 6-row, 2-row, intermediate, etc.), but were found in a few cases in all the F_2 types. Abnormal forms were often difficult to classify, and this may possibly be the reason for the very considerable divergence from the 3:1 ratio—a ratio for which the remaining crosses vouch.

Cross No. 45.

Russian Chevallier, No. 7 × English Archer

2-row	}	2-row
Smooth	}	Bristly

F_1 = all bristly

F_2 = 546 plants. Bristly : Smooth = 410 : 136
= 75.1% : 24.9%

The agreement with 3:1 expectation is thus extremely close.

Cross No. 35.

Russian Goldthorpe, No. 10 × Inerme

2-row	}	2-row
Smooth	}	Bristly

F_1 = 30 plants; all bristly

F_2 = 510 plants. Bristly : Smooth = 387 : 123
= 75.8% : 24.2%.

Here again, the deviation from 3:1 expectation is well within the standard error.

From the above results it is concluded that :

- (a) One factor governs type of hair in rachilla.
- (β) "Bristly" is dominant to smooth, the F_1 being apparently identical with the "bristly" P_1 .
- (γ) Possibly this same factor also governs the type of hair in the glume, rachis segment, and lodicule.

II. THE LATERAL FLORET.

The barleys, i.e. the sub-species of *Hordeum sativum* Pers., are placed in primary groups in accordance with the forms of their lateral florets. In hybrid generations are encountered lateral florets of forms other than those which characterise the recognised "varieties" or sub-species of the barleys. To facilitate the description of hybrid generations there is given [(A)—(G) below] an account of all of the

forms of lateral floret which have been found in those F_2 's and their parents, with which this paper deals.

The various forms of the lateral floret :

(A) Always fertile (i.e. forming a grain), the grain being nearly as large as that formed by the median floret. The lateral is awned or awnless in strict conformity with the median of the race concerned¹. This form of lateral characterises *H. hexastichum* (the 6-row and 4-row barleys of the agriculturist).

(B) Always fertile under normal conditions but the grain decidedly smaller than that of the median floret.

Two sub-species, viz. *H. Huxtoni* and *H. transiens*, possess this form of lateral, and they constitute the race *H. intermedium*. In them, the outer palea of the median bears a long awn while that of the lateral is completely awnless, being rounded at the tip. Under adverse conditions it not infrequently happens that some of the laterals—or even all—fail to set grain. They are, nevertheless, quite perfect in stamens and ovary, and the non-fertility is purely a physiological response to environment; it has absolutely no genetic significance.

(C) Fertile; grain small, smaller than in the case of (B); outer palea terminating in an awn which may be merely a point or up to 3 cm. long. This type is confined to hybrid generations and appears to be a heterozygote.

(D) Non-fertile but inflated; the outer palea pointed or shortly awned. Like (C) it occurs only in hybrid generations and (see below) is probably a heterozygote. Stamens and a reduced ovary are present.

(E) Non-fertile but large and inflated; outer palea always rounded and devoid of an awn. Stamens and a reduced ovary are present. This, again, occurs only in hybrid generations.

(F) Non-fertile, of full length, but not inflated. The outer palea is always rounded and awnless. Stamens and a very small shapeless ovary are present. This type characterises the "distichum" barleys to which the familiar malting varieties Archer, Chevallier, Goldthorpe, etc. belong. Changes of environment, however pronounced, appear not to be able to cause this type of lateral to set grain.

(G) Non-fertile and extremely reduced. There is a small outer palea and a vestigial inner one, but no traces of rachilla or reproductive organs are to be seen. This is the Abyssinian or "decipiens" type.

¹ The 6-row type devoid of awns in both median and lateral florets is exemplified by the variety "Nogenasi" which Ikeno (9) employed in a cross to determine the inheritance of awns.

This classification of the forms of the lateral floret, although adequate for the recognised natural races of barley, cannot be infallibly applied to hybrid generations, even when types (C), (D) and (E) are employed. The late tillers of a single plant may differ from the early ones, and upon any ear more than one type of lateral floret may occur, e.g. (C) and (D), (D) and (E), etc.

The exact morphology of (F) and (G) will have to be determined by sections of developing ears at successive early stages.

Hordeum inerme—an awnless distichum obtained first by Rimpau from the cross *H. Steudelii* \times *H. trifurcatum*—offers many complexities when used in crosses, in connection with the form of the natural floret. Results so far obtained upon certain F_2 's in which *H. inerme* has been used, have not given absolutely consistent results, and consequently they are not included in this paper. *H. inerme* appears to be the key to the problem of inheritance of several characters, e.g. lateral floret and awns.

Details concerning the classification by form of lateral floret are to be found in any systematic account of the cereals. The most practicable classification appears to be that of Beaven (3).

III. THE INHERITANCE OF THE LATERAL FLORET.

Observations have been made upon a considerable number of crosses between 6-row and 2-row (distichum) barleys. In the notation of § II above these may be represented by (A) \times (F). In some cases reciprocal crosses were made, but as both directions of the cross gave the same result—a fact established by Biffen (4) and (5) for many barley crosses—the ♂ and ♀ parents are not separately designated in the tables of results.

At the outset, an attempt was made to classify in the F_2 's all the various forms of lateral which were neither (A) nor (F). Table I

TABLE I. *Six-row* \times *Two-row*.

No. of Cross		F_1	F_2 (type of lateral)				
			(A)	(B)	(D) Awned	(D) Pointed	(F)
43	6-row Praecox \times 2-row Archer	Laterals bearing a short awn. On every ear a few laterals set grains	129	9	80	171	118
57	6-row Praecox \times 2-row Plumage	As for F_2 . 43	48	39	30	30	39
58	6-row Praecox \times 2-row Archplume	Laterals large and sharply pointed but none set grain	108	47	← Total = 280 →		

contains the results of some of the attempts, the notation for the types of lateral floret being that of § II above. It is apparent that the relations of the frequencies of the (B), (D)-awned, and (D)-pointed classes are not constant, and the conclusion is that these classes are not constantly and genetically different. In the light of the facts of fluctuation mentioned in § II (B) above, the simplest view to adopt is that these three classes are genetically identical, and that their apparent differences represent the effects of environmental irregularities. Biffen (4) in the case of the cross *H. Schimperianum* (6-row) \times *H. nutans* (2-row) has completely justified this view by proving that all F_2 plants which were neither (A) nor (F) gave, in spite of eye differences *inter se*, F_3 families containing (A), (F) and various forms of the (D) type, i.e. that all such F_2 plants were heterozygous in respect to one factor, for form of lateral floret.

In consequence of this conclusion, the remaining F_2 's were classified by grouping all the (A) plants and the (F) plants, and combining the balance of the F_2 under the name "heterozygote." Table II gives, in

TABLE II.

No. of Cross	Parents	F_2 types of lateral floret		
		(A) i.e. 6-row	Heterozygote	(F) i.e. 2-row
43	6-row Praecox \times 2-row Archer	129 25.4% $\pm 1.9\%$	260 51.3% $\pm 2.2\%$	118 23.3% $\pm 1.9\%$
57	6-row Praecox \times 2-row Plumage	48 25.9% $\pm 3.2\%$	99 53.1% $\pm 3.7\%$	39 21.0% $\pm 3.2\%$
1	6-row Trifurcatum \times 2-row Archer	46 26.7% $\pm 3.3\%$	83 48.3% $\pm 3.8\%$	43 25.0% $\pm 3.3\%$
2	6-row Victoria \times 2-row Archer	50 23.6% $\pm 3.0\%$	109 51.4% $\pm 3.4\%$	53 25.0% $\pm 3.0\%$
4	6-row verbessert \times 2-row Archer	55 26.2% $\pm 3.0\%$	94 44.8% $\pm 3.4\%$	61 29.0% $\pm 3.0\%$
5	6-row Frühling's \times 2-row Archer	49 21.6% $\pm 2.9\%$	123 54.2% $\pm 3.3\%$	55 24.2% $\pm 2.9\%$
6	6-row Nachte kleine \times 2-row Archer	21 21.7% $\pm 4.4\%$	53 54.6% $\pm 5.1\%$	23 23.7% $\pm 4.4\%$
Totals ...		398 24.8% $\pm 1.1\%$	821 50.9% $\pm 1.2\%$	392 24.3% $\pm 1.1\%$

this form, the data of several crosses. In this table, for every cross, the first row shows the actual numbers of plants in the (A), heterozygote, and (F) classes. The second row contains these numbers expressed as percentages, while the third row shows the standard errors of these percentages due to fluctuations of sampling. The standard errors have been calculated on the basis of an expectation of 1:2:1, i.e. 25%:50%:25%. The table contains twenty-four percentages, and in five cases only does the difference between observed and calculated percentages exceed the standard error, whereas some seven cases might be expected. The cases are as follows:

Cross 57	...	21.0%	instead of	25 ± 3.2
Cross 5	...	21.6%	„	25 ± 2.9
Cross 5	...	51.2%	„	50 ± 3.3
Cross 4	...	41.8%	„	50 ± 3.4
Cross 4	...	29.0%	„	25 ± 3.0

It is not easy to sort such an F_2 for type of lateral floret. In stunted plants the difference between (F) and "heterozygote" is much obscured. Consequently there seems justification for stating that the results of the crosses indicate the proportions (A):heterozygote:(F) = 1:2:1 in F_2 . The combined results of the crosses (last row of Table II) show no deviation as great as the relevant standard error.

To summarise these conclusions it may be said that:

(a) Six-row and two-row (distichum) barleys differ in regard to form of lateral floret by one factor only.

(β) The heterozygotes of F_2 resemble the F_1 plants. Like them they are subject to fluctuations induced by environment. These fluctuations result in apparent differences, but constantly different groups cannot be found.

Blaringhem (10) has introduced novel views in connection with crosses between 6-row and 2-row barleys. In the appendix (p. 106) attached to this paper will be found some observations upon his views.

v. Ubisch (6) has made extensive observations upon 6-row × 2-row crosses and has formulated a hypothesis on the assumption of a two-factor difference between the parents in regard to form of lateral floret. He found that the laterals of the F_1 plants, like those of the F_2 heterozygote plants, were much influenced by conditions. The classification adopted for the F_2 was

zwei-zeilig : zwei- bis sechs-zeilig : sechs-zeilig.

The middle class was thus defined: "Es hat sich als zweckmässig zur Analyse herausgestellt, allen Typen, die gelegentlich fertil sind, als zwei- bis sechszeilig zu bezeichnen."

In the 2-bis-6 class were found several types, such as "Spitz," "Spitz verlängert," etc., and consequently, although he recognised that the F_2 ratios were monohybrid, he thought it desirable to employ a di-hybrid or 2-factor explanation, because of the diversity of the heterozygote forms. The fit of observation to expectation is good. As factors were employed: Z , which is responsible for the 2-row state; W , an intensifier which is operative only in the presence of Z , and in the absence of which there is an "Übergehen" from 2-row to 2-6-row. In the light of the evidence furnished by the crosses described in this paper, two points of v. Ubisch's theory appear not to harmonise with the facts of observation. These are:

(α) Plants of the constitution $ZZWw$ and $ZZww$ are described as 2 bis 2-6 zeilig. This seems to imply that 2-zeilig is not genetically a definite group. The evidence of Table II demands that it should be of definite and invariable genetic constitution.

(β) The ratio 6-row : all others is stated to be 1 : 3. In Table II the ratio 2-row : all others also appears to be 1 : 3. v. Ubisch however finds that the proportion of 2-row : all others is 3 : 13. This divergence from the results recorded in Table II is, of course, simply a consequence of (α) above.

IV. THE PROBLEM OF INHERITANCE IN LATERAL FLORETS.

As described in § II, the lateral florets found in the various races of barley, and in their crosses, form a series (A)—(G). There is reason to believe that (B), (C), (D) and (E) are genetically alike in regard to constitution for the development of reproductive organs. Probably there occurs a further series, corresponding to (B), (C), (D) and (E), and produced by crosses between decipiens and distichum types (see below).

The evidence which has accumulated up to date concerning the general question of lateral floret inheritance in barleys seems sufficient to justify a brief review. Much of it has already been published by Biffen (4) and (5). In these publications will be found the details of those cases which are simply recorded in outline below. The four sub-groups of barley—hexastichum, intermedium, distichum, decipiens—together with the interesting awnless *H. inerme*, permit of ten sets of crosses, and these are now described serially:

(α) *Hexastichum* \times *intermedium*, i.e. (A) \times (B).

In all cases the F_1 had six complete rows of fertile florets, but the

laterals were less strongly awned than were the medians [Hexastichum barleys have their medians and laterals fully awned; intermediums have fully awned medians and completely awnless, blunt-ended laterals].

Cross No. 14—*Haxtoni* \times *pyramidatum*—was worked out fairly completely. In the F_2 the following proportions were found:

Typical 6-row : Remainder of F_2 = 43 : 133

(all awns full) = 1 : 3

The "remainder" consisted of some plants exactly resembling the F_1 , of some with part only of their lateral florets fertile and with their lateral outer paleae sharply pointed, and of some with occasional fertile laterals, the lateral outer paleae being always blunt (as in the Haxtoni parent). From the F_3 it was clear that the "typical 6-row" of the F_2 was homozygous, as was the F_2 group which resembled Haxtoni. The F_2 group, whose lateral paleae were pointed, produced in F_3 all types (the two parental and the pointed lateral). They were therefore heterozygous. The variability of the shape and fertility of the lateral—common in heterozygotes—made precise sorting very difficult, and the proportion of Haxtoni type in F_2 could not satisfactorily be proved to be $1/4$ (actually it was 21.1%). That the Haxtoni type of F_2 bore some infertile laterals on certain (or all ears) of some plants, is in conformity with the fact that precisely the same thing may and often does occur in pure parental Haxtoni.

The definiteness of the 1 : 4 proportions of pure 6-row type in F_2 (43 plants out of an F_2 of 176 plants) and the approach of the proportion of Haxtoni plants in F_2 to 25%, point to the fact that the difference between the parental forms is, for lateral floret, unifactorial.

It may therefore be stated—using the notation of § II above—that the lateral floret forms (A) and (B) are allelomorphs.

(β) *Hexastichum* \times *distichum*, i.e. (A) and (F).

The evidence of § III shows that (A) and (F) are allelomorphic characters.

(γ) *Hexastichum* \times *decipiens*, i.e. (A) and (G).

The data given by Biffen (5) show that in the F_2 a 1 : 2 : 1 ratio was obtained.

The F_3 growings afforded full confirmation of the fact that the F_2 contained, in addition to both the parental forms, one and only one heterozygote.

Hence (A) and (G) are allelomorphic characters.

(δ) *Hexastichum* × *distichum* (*H. inerme*).

Consistent results have not been obtained. The extreme fluctuation to which *H. inerme* is liable in response to climatic change no doubt largely accounts for this lack of consistency. One fact of great interest has, however, been established. In the F_2 , the combination 6-row-awnless does not occur. The inter-relation between six fertile rows and the absence of awns which this fact implies, has yet to be discovered.

(ε) *Intermedium* × *distichum*, i.e. (B) × (F).

Several such F_2 's were raised in the summer of 1919, but the extreme drought of the early part of the flowering period produced great fluctuation. The ears of the single plant differed markedly among themselves in some cases. It seems that here, too, a 1 : 2 : 1 ratio is likely to be found, but the complete F_3 's of 1920 will have to be awaited for a confirmation of the anticipation.

(ζ) *Intermedium* × *decipiens*, i.e. (B) × (G).

Crosses between *H. gymnospermum* (awned, black, *decipiens*) and *H. Haughtoni* (typical *intermedium*) indicate that the F_2 consists of the two parental types, and a heterozygote type. Sorting is too difficult to give reliable proportions. The allelomorphism of (B) and (G) is not therefore properly established.

(η) *Intermedium* × *distichum* (*H. inerme*).

Cf. (δ) above. Here too emerges a fact of some interest. The proportion of awnless types is extremely low. The awn is subject to very great fluctuation, e.g. from ear to ear of a plant, and F_3 's will be necessary before any definite result can be reached.

(θ) *Distichum* × *decipiens*, i.e. (F) × (G).

The 1 : 2 : 1 ratio has been well established; hence (F) and (G) are allelomorphic characters.

(ι) *Distichum* × *distichum* (*H. inerme*).

Only by complete F_3 's (to be grown in 1920) can this cross be properly studied.

(κ) *Decipiens* × *distichum* (*H. inerme*).

No observations are available.

The above categories of crossing results may be summarised thus :

The following have been shown to be pairs of allelomorphic characters:

(A) and (B), see (α).

(A) and (F), see (β).

(A) and (G), see (γ).

(F) and (G), see (θ).

The following may also prove to be pairs of allelomorphic characters:

(B) and (F), see (ϵ).

(B) and (G), see (ζ).

The various forms of the lateral floret in barley thus appear to afford another instance of the phenomenon which is now known as "multiple allelomorphism." The work of Morgan on eye-colour in *Drosophila*, the coat-colour of mice, colour in the maize cob, silk, etc., and the experiments of Nabours (8) on *Paratettix* afford further evidence of this phenomenon—a phenomenon which, other things apart, is of great interest because of its failure to harmonise with the "presence and absence" hypothesis (in its simple form and without appeal to complex linkages).

Few instances of genetically related degrees of development appear to be so evenly graded as that which has been described here, and a good opportunity presents itself for an attempt to correlate "Mendelian characters" with morphological structures. Such an attempt would have to be based upon a histological study of the various forms of lateral floret at successive developmental stages. The difficulties imposed upon the sorting of F_2 types by fluctuations due to environment are very great, and it is unlikely that they will be completely surmounted without a histological study of this kind.

Appendix. Some observations upon the views presented by Blaringhem (10) concerning the results of certain crosses between 6-row and 2-row barleys.

Blaringhem has insisted upon the occurrence and upon the importance of "L'Hérédité en mosaïque" (or "Naudinienne"). He has cited the following 6-row \times 2-row barley cross as an example.

H. tetrastichum pallidum was crossed with *H. distichum nutans*. The F_1 consisted of "plantes vigoureuses offrant toutes des épis à deux rangs." No more detailed specification of F_1 characters was recorded. In F_2 there were 410 plants. The 6-row type numbered 134, and they were "presque aussi nombreuses que les plantes à deux rangs"; but what was accepted as the most striking thing about these 6-row plants

from F_2 was the fact that at the base of the ear they were 6-row, while at the upper end they were 2-row. In other words, they represented "mosaic inheritance."

A number of objections have to be lodged against these conclusions:

(1) "à deux rangs" is, in such a case, too vague a description to carry any strict classificatory meaning. It has repeatedly been observed that the F_1 plants of a 6-row \times 2-row cross while invariably possessing large fertile median florets, have variable laterals. The laterals may all be simply large, pointed, and inflated (as compared with those of genuine 2-row barley); but very commonly a certain small proportion of them on any ear sets grains. The variability is considerable, but the distinction from pure 2-row is always apparent. The descriptions employed are so vague that there arises doubt as to whether the precise differences between heterozygous and homozygous (2-row) were considered.

(2) The proportions of types recorded for the F_2 are such as do not appear among the numerous other recorded results.

Thus, 2-row : total F_2 = 134 : 401 (about).

From the statements made in the text the expectation is

$$100 : 400.$$

If plants of homozygous type, which owing to conditions had failed to set any lateral grains, were classed as "à deux rangs," then an excess of 2-row was certain to result. Moreover if *all* plants having *some* fertile lateral florets were regarded as "6-row," this category was certain to include some of the heterozygotes (which are like F_1) and again an excess over the 1 : 4 expectation is to be anticipated.

(3) In the text the extreme susceptibility of the sexual organs of potentially fertile lateral florets has been explained. The consequent variability—some fertile and some non-fertile laterals on the same ear—is so great, and so commonly exemplified in F_1 's and F_2 's, that without a very critical examination no conclusion as to "mosaics" seems warranted. Clearly every ear which Blaringhem classed as 6-row in his F_2 was not a "mosaic"; but the amount of mosaicism cannot be gauged from the record "presque toutes offraient la mosaïque des caractères."

(4) The opinion that the so-called "mosaics" were simply heterozygotes is confirmed by the fact that grains collected from the "2-row part of the ears" and also those collected from the "6-row part of the ears," both gave all three ear-types when sown.

(5) Variation in the form of the mosaic is yet another indication of ordinary lateral-floret "sterility" (better, "non-fertility"). Whereas, in general, the mosaic was of the type "6-row base and 2-row tip" there were found some ears 6-row all down one side and 2-row all down the other. It is not stated whether or not each kind of "mosaic" bred true and whether or not both types could occur upon a single plant. These questions of circumstantial fact are very important.

On p. 246 (10) a somewhat revolutionary conclusion is recorded. Crosses between closely allied lines exhibit Mendelian inheritance: those between distant lines ("du mélange d'espèces linnéennes distinctes—nutans, erectum, nudum") are characterised by ratios differing from those required by Mendel's Laws. These deductions were made with reference to crosses in which the experimental character was "projections on the nerves of the palea." It is to be observed that many barley crosses have been made and "Mendelian" results recorded, despite the fact that the parents were more distantly related than those which Blaringhem cited. However, the results recorded in connection with Blaringhem's particular character are not such as to afford, of themselves, a refutation of the above conclusions. [The inter-specific crosses among the wheats furnish perhaps the best collection of evidence in refutation of the conclusions.]

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