MENDEL'S LAWS OF INHERITANCE AND WHEAT BREEDING.

By R. H. BIFFEN, M.A.,

Botanist and Lecturer in Agricultural Botany, Agricultural Department, Cambridge University.

THE investigations to be described below are the outcome of some experiments started in 1900 which had in view the improvement of English-grown wheat. The necessity of such work may not be evident to all, so at the outset I will sketch in broad outlines the state of affairs which led me to undertake the task. The fact is generally recognized that the wheats of this country are characterized by their high yields per acre and by the shapeliness of their grain. We can grow on the average over 30 bushels to the acre where the United States grow 14, Russia 10, and the Argentine 7. Yet the acreage under wheat in this country has fallen from three and a-half million acres in 1876 to one and a-half million in 1903, and we now grow approximately only one-fifth of the wheat we consume. Further than this there is good evidence to show that the quality of the grain now grown is inferior to that of twenty years ago[1]. It has been sacrificed to yield, and many of the better class varieties, such as Chiddam, Red Lammas and Rough Chaff, have been more or less driven out of the field by varieties such as Square Head and Rivet, which are capable of giving slightly larger crops of grain and straw. These inferior varieties have now to compete with wheat imported from Canada, the United States, Russia and other countries. The seriousness of the position becomes evident when one finds English wheat selling at 28*s*. 6*d*. a quarter when Manitoba Hard is selling at 35*s*.[2]

[1] Girard and Lindet, *Le Froment et sa Mouture*, Paris, 1903, p. 101.

[2] The figures are a general average—they do not refer to the abnormal prices of this season.

On searching for the reasons of this, the miller tells us that English wheat, even of the better class varieties, is lacking in "strength." We have no single variety which can be compared in this respect with the best foreign wheats. By "strength" he means the capacity of the wheat to produce a large, well-piled loaf[1]. We learn also that English wheat to be utilized at all for bread-making purposes has to be mixed with a large percentage of these strong foreign wheats. The flour of English-grown wheat, alone, will not produce a loaf which is marketable under present conditions, and until the public taste demands dull and heavy bread such wheat can only be used in mixtures.

In addition to this another complication has to be faced. Since the opening up of the wheat-growing districts of the United States and Canada, which in itself has given us an altogether new standard of strength in wheat, the milling trade has to a large extent found its way to the ports. The millers so situated grind the strong wheat brought direct to their mills by sea. The inland miller on buying foreign wheat to mix with our inferior grain has to pay railway freightage, and at present his very existence depends on the fact that he can buy English wheat relatively cheaply at his doors. If, in order to compete with the port miller, he has to use still larger quantities of foreign grain to make up for the shortcomings of our own, then prices must fall still lower or he will be driven out of the field and with him will disappear the market for home-grown wheat. The whole question then pivots on the strength of the grain we can produce. Even a slight increase in quality would go a long way to improving the position both from the farmer's and miller's point of view, for it would immediately widen the market for the home product[2]. Unfortunately we know very little as to what constitutes strength in grain. Many attribute it solely to climatic conditions and state that our problem is a hopeless one. Without discussing the matter I may point out that the work of the Home-grown Wheat Committee of the Incorporated National Association of British and Irish Millers has ruled this view out of court. We can grow strong wheat in this country, but so far the cropping power of the varieties tried has been so poor that the operation has generally resulted in loss. Realizing as I do the complications of the problem I prefer to make no definite statement as to the progress

[1] See also Maurizio, *Getreide, Mehl und Brot*, Berlin, 1903, and *Landw. Jahrb.* Bd. XXXIII. Heft II. p. 242, 1904.

[2] For further evidence see Hall, "The Quality of English Wheat," *Journ. Farmers' Club*, 1904, p. 123, and *Journ. Board of Agric.* 1904, p. 321.

we have made so far. Several years must elapse before sufficient quantities of the grain of the new varieties can be obtained to subject to the final tests of the mill and bake-house. We can but hope that among the hybrids on the experimental plots are some that will not be found wanting when these trials are made.

At the time of starting these experiments hybridizing was, to quote Lindley, writing over 50 years ago, "a game of chance played between man and plants." Looking at what literature there was dealing with the subject the chances seemed in favour of the plants. The enormous number of varieties of wheat in existence has originated, as far as we have any reliable evidence, in a similar way to the varieties of other plants. Now and then an observant person has detected a plant among the crop differing from its fellows in some character which made it worthy of further propagation. Foremost among such observers was Patrick Shirreff, who discovered many of our older varieties. They have not been built up, as is generally assumed, by a process of accumulative selection, they are rather "mutation" forms[1]. Very few, as far as we have records, have attempted to bring about improvements by cross-breeding. Thus Vilmorin has described the results of crossing together a number of the sub-species of *Triticum sativum*[2]. Rimpau in his classical memoir "Kreuzungprodukte landwirthschaftlicher Kulturpflanzen," has described the results of many years' experimenting in this direction[3]. Some few hybrids were raised in the Minnesota Wheat-breeding experiments[4]. In addition to this more scientific work some seedsmen have also attempted to raise the standard of the varieties of wheat by cross-breeding. In this country the work of the Gartons, which has resulted in the introduction of a number of fresh varieties, characterized on the whole by high-yielding properties, is the best known. Little beyond popular descriptions of their work has, however, been published. An examination of the literature existing at this date, 1900, gave one no clue as to the best methods of attacking the problem. A considerable number of crosses were therefore made indiscriminately, trusting that some few might give improvements in the required direction.

In 1901, however, the whole aspect of the problem was changed by the simultaneous discovery by three independent observers, De Vries,

[1] See De Vries, *Die Mutationstheorie.*

[2] Vilmorin, *Bull. Soc. Bot. France*, T. xxxv. p. 49, 1888; T. xxvii. p. 73, 1880.

[3] Rimpau, *Landw. Jahrb.* Bd. xx. p. 335, 1891.

[4] *Minnesota Agric. Expt. Stat.* Bulletin 62.

Correns, and Tschermak, of the work on inheritance carried out by Gregor Mendel and communicated to the Brünn Society in 1865. This was published the following year, but judging from the fact that only one reference to it is known, and that one gives slight clues as to its value, it was completely lost sight of[1]. As this remarkable paper shows, Mendel focussed his attention not on the plant as a whole but on its single characters, such as seed-shape, colour, etc., and he traces in detail the behaviour of each character in the cross-bred. Then instead of attempting to generalize from the mass of unlike forms appearing in the first generation from the cross-breds he took each individual and subjected it and its progeny to a statistical examination, again character by character. As the outcome of this series of experiments, which in themselves must in future be the model on which experiments on plant improvements are based, he was able to state that the gametes, the egg-cells and pollen grains, are pure with respect to the characters they carry. If for instance a cross is made between a round and a wrinkled pea the cross-bred produces gametes which bear either the round or the wrinkled character, not a blend of the two. Postulating that an approximately equal number of pollen grains and egg-cells carry either one or the other of the characters, then certain numerical relationships observable in the progeny of the cross-breds find a simple explanation. With this clue on reading such works as Darwin's *Animals and Plants under Domestication*, Focke's *Pflanzenmischlinge*, Gärtner's *Bastarderzeugung*, one saw, though written from a totally different standpoint, that many facts till then the mysteries of the breeder, found a simple explanation. In fact to those familiar with these special problems further evidence was hardly necessary. One saw still further that many of our current theories of heredity had no real foundations, and that at the first critical test they must fail.

To agriculturists who as a class are continually in touch with the problems of heredity, both in stock and crops, exact knowledge of this kind is invaluable. In the case of our problem, for instance, if wheats behaved in the same manner as Mendel's peas, then the fixing of the chosen forms after the "breaking of the type" was going to be a simple matter requiring merely the test of a single season and not years of selection and in-breeding. If this were really the case we had prospects of, so to speak, picking out the valuable characters from different

[1] The original paper in the *Verh. naturf. Ver. in Brünn Abhandlungen*, IV. 1865, is almost unobtainable. Translations will be found in the *Journ. Hort. Soc.* 1901, Vol. XXVI. Parts 1 and 2, and in *Mendel's Principles of Heredity*, Bateson, Camb. 1902.

varieties and building up an ideal type. There were possibilities ahead the breeder had hardly dared to hope for. Fresh experiments on the same lines as those of Mendel's were accordingly planned with the object of obtaining definite knowledge as to the behaviour of all the possible characters of wheat on hybridizing. It is true that much could be deduced from Rimpau's work[1] which now became a mine of information, for from his detailed descriptions one could in many cases see clearly how certain of the characters behaved. Here and there, however, it seemed that complications occurred which would entail further investigations, so it was decided to make the experiments as complete as possible, as even confirmatory evidence has its value. During the course of this work two other papers dealing with wheat appeared. One by Spillman is of unusual interest, as it describes experiments carried out on the same lines as Mendel's though the author was at the time unaware of the fact. The results stated afford a striking confirmation of Mendel's laws[2]. The second by Tschermak again serves to confirm Spillman's results. More detailed references will be made to these in describing the behaviour of the differentiating characters later.

One older reference is not without interest now-a-days[3]. Le Couteur selected from one of his trial plots a peculiarly vigorous, red, velvet-chaffed (felted) wheat. Among the progeny were plants with red and velvet, red and smooth, white and velvet, white and smooth chaff. He counted the total number of ears, not individuals, and found 200, 21, 86, and 43 respectively of each kind[4]. His original plant was evidently a hybrid, probably a first cross as it was so vigorous, which broke up into the forms we now expect. Le Couteur concluded that this velvet-chaffed red wheat was incorrigible and put forward the following theory to account for the facts. "It might be conjectured that the original or parent ear, having been discovered in a field of mixed white corn, had been impregnated by the pollen of four different sorts of wheat, which the peculiar conformation of an ear of wheat might admit."

For a detailed study of Mendel's laws the wheats proved to be peculiarly suitable. They offer all the advantages for which Mendel originally selected peas. Thus there are a large number of varieties in

[1] *Ibid.*

[2] Spillman, *Science*, Vol. XVI. p. 794, 1902; see Hurst, *Journ. Roy. Hort. Soc.* 1903, Vol. XXVII. Part 4; Tschermak, *Zeits. Landw. Versuchs. Oesterreich*, 1901, Heft II. p. 1029.

[3] Le Couteur, *The Varieties, Properties and Classification of Wheat*, Jersey, 1837, p. 65.

[4] Compare p. 29.

cultivation (I have grown over 200) which are singularly constant; they are autogamous with rare exceptions[1]; the hybrids suffer no diminution in fertility during succeeding generations. In addition to this they have the advantage that they occupy very little space and consequently large numbers can be grown on a small plot of ground. Their chief drawback is that they require to be autumn-sown to give the best results. This leaves only a short period between harvest and seed-time to work through characters, such as those of the grain, which cannot be examined before gathering the crop.

The more important differentiating characters of wheat are as follows:—

(1) The ears are dense or lax. Ears are dense in which the spikelets are so crowded on to the rachis that they overlap one another; the internode length (the length of rachis separating each spikelet) being in such cases about 3·5 mms. Such varieties are often described as club, or club-headed wheats. A typical example is Hedgehog[2]. In lax-eared wheats the ears are generally long and in most the top of each spikelet only reaches to the base of the one immediately above it; the internode length is about 7 mms. Between these dense and lax-eared wheats is a third group with compact ears. These divisions are of course arbitrary and one finds many varieties which cannot properly be classed in either. Each variety, however, is singularly true to ear shape.

(2) The paleæ may or may not be awned. Technically they are described as bearded and beardless. Rivet[2] is an example of the former type, Golden Drop[2] of the latter.

The beardless wheats frequently bear small awns on the paleæ of the spikelets towards the apex of the ear. Such awns are usually short, not exceeding half an inch as a rule, and they cannot be confused with the awns of such a wheat as Rivet, where they are 3 or 4 inches in length and borne on every spikelet.

(3) The glumes may be glabrous or covered with fine, velvety hairs as in the well-known wheat Rough Chaff[2]. The softly hairy forms are sometimes described as "felted."

(4) The colour of the glumes and to a less extent of the paleæ may be red or white. "Red" includes a large number of different

[1] I have never met with a case of natural cross-fertilization, but Rimpau cites a number of undoubted examples.

[2] Figured in Vilmorin, *Les meilleurs Blés*, Paris, 1880.

shades varying from pale red to dark brown, whilst "white" is used to describe any shade from white to pale ochraceous yellows. As a rule the difference between red and white is a sharp one, but in a wet season when the chaff is apt to become discoloured it is often difficult to be sure of the colour. Each variety is quite true to its own particular shade of colour.

More rarely the colour of the chaff is grey as in Rivet wheat. This colour is, at least in my material, very variable. Some ears are dark, others light grey, but in all cases the tint is sufficiently marked to be detected with certainty.

(5) The shape of the glumes provides a number of characters used in classifying the varieties. In some of the sub-species into which *Triticum sativum* has been divided, as in *T. spelta*, *T. turgidum*, *T. durum*, the glumes have a well-marked keel running from the apex to the base. In others, such as *T. vulgare*, the sub-species which includes the majority of the varieties in general cultivation in this country, the keel is only pronounced at the apex of the glume, the base being rounded. I have described these types as "keeled" and "rounded" glumes.

(6) The grain colour is either red or white, the terms again being used to denote the range of colours already mentioned in the case of the chaff. These colours may be associated with a similar colour in the glumes. In the majority of the red-chaffed varieties the grain is also red, but a number of white-chaffed varieties with red grain are in cultivation. The converse case of red chaff and white grain is uncommon, though not impossible.

(7) The shape of the grain is frequently very characteristic, so much so that a grain merchant or miller can often identify a variety from its grain shape alone. The differences in general are difficult to describe clearly though they are readily appreciated after a little practice. In the following account grain shape is only considered in detail where very marked differences exist. In this particular case the grains are either long and triangular in section, or short and rounded.

(8) The characters of the endosperm are again difficult to describe. Those most readily recognized are the hard, translucent, and the soft, opaque types. The former type is met with in the macaroni wheats *T. durum* and *T. polonicum*; the latter is characteristic of most of our commonly cultivated varieties.

The difference is in the main associated with the total nitrogen content of the grain, the macaroni wheats containing a higher percentage than our own varieties.

It would appear also that "strength" is often associated with a hard and translucent endosperm, but further evidence is needed, for the macaroni wheats, for instance, are not "strong" wheats from a miller's point of view. In any attempts to estimate these characters it is essential to reject any ears which are not thoroughly ripened. An unripe ear of the normally soft Rivet wheat may yield hard, translucent grain.

In addition to these characteristics a number of others of less systematic importance will be considered later.

The methods of working are described in some detail below. They are the outcome of several seasons experience with this kind of work and may prove useful to others engaged in similar researches. All the plants are grown under large wire cages as a protection against the depredations of sparrows. This precaution would probably be necessary in most districts, for once sparrows begin to attack the plots they only desist when no more grain is obtainable, and the ordinary methods of scaring seem useless when one is dealing with small plots of wheat. The drawback to the use of permanently fixed wire cages is the difficulty of guaranteeing that no shed grains remain in the soil and come up with the next crop. Working the ground as soon as the crop is off and cleaning again a month later partially meets the difficulty, especially if fowls can be turned into the cages to pick up shed grain. A still more effective plan is to alternate the wheat plots with another crop. I now make use of barley for this purpose as similar experiments are in progress with it.

The actual operation of crossing wheats is a simple one and may be carried out rapidly with a little practice. After many trials I have found the following method the most satisfactory. The ear to be operated upon is selected at the stage when the anthers of the median spikelets are full-grown and beginning to show a slight tinge of yellow, indicating that they will be ripe on the following day. If the ear belongs to a dense or a compact variety alternate spikelets are removed on both sides of the rachis, preferably by tearing them off whole with a pair of forceps. The median florets of about a dozen spikelets are then removed by pressing them outwards and then pulling sharply downwards. In this way only the two outermost florets of each spikelet are allowed to remain. The remaining spikelets are then completely removed. The florets are opened by gently pressing the apex of the paleæ, or if a bearded variety is used by pressing outwards the previously cut-back awn, and the stamens are carefully removed.

Should an anther break during the operation the spikelet is cut off. Pollination is effected by immediately placing a freshly opened anther into the emasculated floret. To secure a supply of these an ear of the variety chosen as the pollen-parent is selected in which the anthers are a full yellow colour. The edges of the spikelets are trimmed off with a pair of scissors so as to open a number of the florets at the apex. The filaments of the mature stamens elongate in the course of a few minutes and push the anthers out of the opening at the apex of the paleæ. They split open and by inserting one top downwards into the emasculated floret a plentiful supply of pollen is showered on the stigma. Before making a fresh set of crosses, or in the event of a stamen from the mother-plant breaking, the forceps are sterilized by dipping them into methylated spirit. There is no necessity for removing the stamens from a floret and pollinating the following day, nor yet of carrying out the operation at an early hour in the morning. If there is any difficulty in securing the varieties in flower at the same date it is feasible to remove the stamens from the earlier variety and protect it from outside pollen. I have never examined the matter in any detail but I have frequently pollinated flowers successfully a week after the stigmas would normally have been in a receptive condition. They were then feathery and unwithered. After pollination the ears are protected by means of folded tissue-paper bags previously waterproofed by soaking in melted paraffin wax. Numerous control experiments have shown that muslin bags are unsuitable for the purpose. An ear for instance on which 12 emasculated florets were left was covered with muslin. Each floret set a grain, pollination having been brought about by wind-borne pollen carried through the meshes of the muslin. The protecting bags may be removed a week after pollination or they may remain on the ears until the grain ripens. If the latter course is adopted the bags should be slit open at the base to allow the water to escape which accumulates, as the result of transpiration, in considerable quantities.

The artificially fertilized grains usually mature a day or two earlier than those naturally fertilized. They are frequently, but by no means always, poor and shrivelled in appearance, but they rarely fail to germinate. Working in this way it is not unusual for 90 per cent. of the artificially pollinated florets to set grain, but much depends on weather conditions. In 1903, for instance, most of the pollinating had to be done on plants sheltered from the rain by tarpaulins. Three per cent. only were successful.

The cross-bred grains are sown as early as possible and given as much space as is convenient in order to secure plentiful tillering.

In the earlier experiments the ears of the resulting plants were enclosed in paper bags or test-tubes to make sure that no extraneous pollen reached them. A series of control experiments showed that this was unnecessary and now they are simply left exposed. The most striking feature of these plants is their unusual vigour. Many have been over 7 feet high when mature, and one could as a rule detect plants resulting from accidentally self-fertilized grains by their lack of vigour when compared with their hybrid neighbours. The grain from the cross-breds is planted in ranks 2 feet long, 12 grains to each, and 8 inches apart. A space of 2 feet between each row of ranks is left as a pathway. By adopting this method the crop is readily cleaned and one can move about among the plants to examine them. Where the cross is between varieties differing only in a single pair of characters a sowing of about a hundred grains is ample to ensure all the possible types occurring among the progeny of the cross-breds. Where one is dealing with more complex cases it is well to sow as much as possible, limiting the crop only by the amount of space and time at one's disposal. Even then the crops are found to increase to such an extent with succeeding generations that much, of necessity, has to be abandoned. In cases where a considerable number of crosses has to be dealt with the entering up of the results becomes no small labour. I have found the following method satisfactory and convenient. A number is assigned to each cross in the notebook, the numbers running consecutively. The hybrid grain is sown and labelled with this number and the characters of the resulting plant noted under it. Each individual of its progeny in turn is assigned a second number, say 8—1, 8—2, 8—3, etc., and its characters are noted on squared paper. The individual numbers are placed successively in a vertical column, and opposite them the characters are noted by a mark in vertical columns reserved for each character, such as bearded, beardless, red, white, etc. In this way a record of each individual is kept with the minimum trouble and the statistical examination is simply effected by adding up the marks in each vertical column. No further numbers are as a rule necessary, as the following generation shows whether the individuals sown under these numbers will breed true or not.

Before giving a systematic description of the hybrids it may possibly simplify matters for those unfamiliar with such work if the story of one or two of the simpler cross-breds and their progeny is followed out step by step. At the same time it may serve a useful purpose if here and there I indicate the bearing of the facts, as they are elucidated, on conceptions still current among breeders. As a simple example we may choose the case of a cross between Bearded White and Stand-up White (Carter's). The only difference between these varieties is that the former is bearded, the latter beardless. The resulting hybrid (called for convenience F_1) is as beardless as the Stand-up White (Plate I. fig. 1); there is no blending of the beardless and bearded characters resulting in a half-bearded ear. Further, the sex of the parent carrying the beardless character makes no difference, for reciprocal crosses give precisely the same result. I have tested this many times and found no exception to the rule. The fact is worth comparing with the older views on prepotency still current among breeders, who frequently treasure the belief that the female parent determines the constitution of the hybrid, whilst the male imparts such attributes as size and colour, in spite of the fact that even in pre-Mendelian days the evidence against this view was overwhelming[1]. No one can say from the appearance of a hybrid which was the male and which the female parent. It is also considered that the phylogenetically older character is the one which appears in the cross-bred. Speculations as to descent have even been based on this view. One has to admit though that our knowledge of the relative age of plant characters is in most cases very meagre, and there are a number of marked exceptions to this generalization.

Where the beardless plant is the female then the cross-bred has precisely the same general appearance (though more vigorous) as its maternal parent, and we have the well-known phenomenon of "skipping a generation"—so called because the crossing apparently has no effect in this generation, though as will be shown it has in the next. Mendel terms the character which appears in the cross-bred to the exclusion of the other a "dominant" character, and the one which is apparently lost a "recessive" character. Thus the beardless condition is dominant over the bearded. Many pairs of differentiating characters however are not sharply dominant or recessive, as will be shown later. Without thrashing old straw it may at once be noted that the phenomena of dominance are of very secondary importance[2].

The grain resulting from the self-pollination of the flowers of the cross-breds produces plants (the F_2 generation) which are either beard-

[1] Focke, *Pflanzenmischlinge*, Chap. IV. p. 469.

[2] See Weldon, *Biometrika*, I. 1902, Pt. II. and Bateson, *Mendel's Principles of Heredity*.

less or bearded, and a statistical examination shows that they occur in approximately the ratio of three of the dominant to one of the recessive forms, or $3D$ to $1R$. The plants showing the dominant character (lack of beards) are all precisely similar as far as external appearances go, but if the progeny of each individual (the F_3 generation) is examined separately it is found that only one-third of them reproduce the beardless character purely, whilst two-thirds produce both beardless and bearded offspring in the proportion of three of the former to one of the latter. The bearded plants of the F_2 generation, that is the recessives, all breed true. If we take a hundred plants at hazard from the progeny of the cross-bred (F_1) they consist not of 75 individuals with the pure dominant character and 25 with the corresponding recessive, but of 25 pure dominants, 50 similar in constitution to the cross-bred as they give the same types of offspring in the same proportions, and 25 pure recessives. We may write this generation then as $D - 2DR - R$. Further generations show that the extracted dominants represented by D and the corresponding recessives R breed true, as far as we can see, indefinitely. The following explanation of the phenomena is offered by Mendel. The two kinds of gametes of the cross-bred bear *either* the beardless *or* the bearded character, *either* D *or* R. If these are produced in approximately equal numbers, then when self-fertilization occurs the chances are that a D pollen grain may meet a D or R egg-cell, giving rise to an embryo, either with dominant characters only or a hybrid, constitutionally represented as D or as DR. Similarly an R pollen grain may give rise to R or DR embryos according as to whether it mates with an R or D egg-cell. No other combinations are possible, so the progeny would be represented by a series of individuals gametically constituted as $D - 2DR - R$. The D and R types breed true, as their gametes carry only dominant or only recessive characters, whilst when the gametes of the type represented as DR, that is the hybrid, are differentiated, then they are segregated into D's and R's, and consequently on self-fertilization the $D - 2DR - R$ series is again produced. Mendel himself tested the point as to the purity of the gametes with respect to the characters they bore by crossing hybrids with the pure dominant and recessive forms, obtaining, as would be expected, in the first case all dominant individuals [$D(D+R)$ gives D and DR], and in the second case equal numbers of dominant and recessive individuals [$R(D+R)$ gives $DR+R$][1].

[1] For further proofs see *Evolution Report of the Roy. Soc.* Pt. I.

We may now consider the results of crossing together two varieties differing in two pairs of characters, such for instance as Rough Chaff and Golden Drop. The former has a white, felted chaff, the latter a red, smooth one[1]. The hybrid (F_1) is rough and red, so that smoothness and whiteness are recessive characters, roughness and redness dominant. For the sake of convenience we may call roughness and smoothness A and a, redness and whiteness B and b. The gametes carry each of these characters pure, and their possible combinations are to be found by combining $A - 2Aa - a$ and $B - 2Bb - b$. These are AB, Ab, aB, ab, $2AaB$, $2Aab$, $2ABb$, $2aBb$, $4AaBb$. There are therefore in F_2 nine types possible, but to the sight only they appear as four, namely, rough red, rough white, smooth red, smooth white in the proportion of 9 : 3 : 3 : 1. The actual numbers obtained were unusually even, being 45 : 16 : 15 : 5 in a total of only 81 plants. The rough red types are represented by AB, $2AaB$, $2ABb$, $4AaBb$, since A and B are dominant over a and b respectively. The smooth red types are represented by aB and $2aBb$; the rough white types by Ab and $2Aab$, and the smooth white by ab. This accounts then for the ratio of 9 : 3 : 3 : 1. The following generation (F_3) shows that the F_2 generation is composed of individuals having the constitution given above. The rough red individuals produced either all rough reds (AB), rough and smooth reds (AaB), rough reds and rough whites (ABb), or rough red, rough white, smooth red, and smooth white individuals ($AaBb$). The rough white individuals either bred true (Ab) or produced rough and smooth whites (Aab). The smooth red individuals either bred true (aB) or produced red and white smooth chaffed forms (aBb), whilst the smooth whites (ab) all bred true.

These results will serve to explain several of the difficulties of the breeder. The F_2 generation, in which the rough red, smooth red, rough white, and smooth white forms appear, represents the well-known "breaking of the type," which we now see is a rearrangement of the characters of the parents[2]. At the same time the fact is explained that the more violent the cross the greater the "variation" produced, since this implies a cross between very unlike varieties, consequently showing many pairs of differentiating characters. It has always been recognized that it is more difficult to obtain "fixed" types from such crosses than from simpler ones. The process may be illustrated by this cross as it is not a complicated one. Four types are distinguishable in the F_2

[1] They have white and red grain respectively, but for the time we will neglect this difference.

[2] In certain cases complications occur: see *Evol. Report*, Pt. I. p. 142.

generation, two of which resemble the parents, whilst two are new, namely, the rough red and the smooth white. A breeder seeking new varieties would probably select the rough chaffed red, a type which is very rare among existing wheats. This type is the commonest in this generation, being represented by nine plants out of every sixteen. Should he select any single individual it might be one of those represented as $4AaBb$, $2AaB$, $2ABb$, or AB. The chances would thus be eight to one against his selecting that represented as AB, the only one which will breed true. On the other hand, should he select promiscuously fine ears here and there, and that is the common method, the plants next season would undoubtedly consist of mixed types. Further selection on the same lines would give the same results, so that one can well believe that certain varieties of hybrid origin have taken years to fix. Where they have been got true it has been chiefly a matter of chance that *DR* forms have been suppressed. Should the breeder have decided to cultivate the smooth white type *ab* it would have bred true from the outset. Here then is the converse case of a fixture being obtained at the outset from the "variations" produced on breaking the type. It is generally believed that rigorous in-breeding will serve to fix a type, but obviously enough the in-breeding of a rough red type with a constitution represented by $AaBb$, say, can never make a fixture of it. It is true that most of its progeny would be rough and red, and that fact would be taken as demonstrating that a gradual approach to fixity of type was being obtained, but nevertheless the only fixture would be the type represented gametically as AB.

One other consideration must be noted. In F_2 the rough white and smooth red forms which appear are identical with their parents. Further they may be obtained as fixtures. Similarly from more complex crosses, when Rivet wheat was one of the parents, in the F_2 generation I have picked out a pure Rivet type and bred it true for two seasons. No one so far can distinguish this Rivet wheat from its parental form. In other words, among the progeny of cross-breds the pure parental forms occur—a fact worth noting by the breeders of pedigree stock. If one were dealing with cattle, would such extracted types be allowed a place among the *élite* of pedigree herds in the herd-book? Pedigree to a breeder implies purity of strain, which means that the individual members comprising it produce gametes of the same types only. Yet in spite of their parentage they would be as pure gametically as those boasting the lengthiest list of "recorded" ancestors.

In addition to crosses between varieties differing in two pairs of characters, three sets of crosses between varieties differing in three pairs of characters have been investigated. The differentiating characters in one case were beardless and bearded (A and a), keeled and rounded glumes (B and b), and felted and smooth chaff (C and c). In F_2 twenty-seven gametically distinct forms are possible, eight of which are fixed, viz., ABC, ABc, AbC, Abc, aBC, aBc, abC, and abc. These fixtures have all been isolated.

An attempt was also made to follow out the progeny of a cross-bred in which four pairs of differentiating characters were united, the three pairs given above and grey and white chaff in addition. Here there should be eighty-one gametically distinct forms of which sixteen would breed true. In the F_3 generation many of the plots produced so few individuals that each type could not be recognized, for where only two or three plants resulted from a sowing of about a hundred seeds it was impossible to obtain the expected number of forms. All the possible fixtures appear to have been produced this season (1904), but in some cases the number of individuals was too small for one to be absolutely confident of the results. Such experiments involve the growing of so many small plots of plants—in this case over two hundred and seventy in the F_3 generation—that they are hardly worth the labour. It would serve no useful purpose to describe each in detail. The results have been recorded throughout, and it is sufficient to say that they are in entire conformity, where the numbers of individuals make this possible, with the results expected from a consideration of Mendel's laws.

Description of Parents.

In the following description of the varieties used in hybridizing, only the more important characteristics are noted. The species *Triticum sativum* (Lam.) has been divided into a number of sub-species, most of which are represented in the varieties described.

Rivet Wheat (syn. Cone or English wheat), *T. turgidum* (Linn.). Ears bearded, felted, compact-dense, square in section, slightly nodding; glumes grey, strongly keeled to the base; grain clear ochraceous red, slightly silky at the apex, starchy and soft; straw long (5 feet), slender, solid or nearly so in the upper internode. Leaves smooth and narrow. It was described by Linnaeus as a distinct species under the name of *T. turgidum*[1]. Now it is generally considered a sub-species of *T. sativum* (Lam.).

[1] Linnaeus, *Species Plantarum*, T. I. Pt. I. p. 478, 1797.

Red King (*T. vulgare*). Ears beardless, glabrous, lax, flattened; glumes straw-coloured, keeled above, rounded below; grain clear ochraceous red, silky at the apex; straw stout, of medium length (4 feet), hollow; leaves broad, scabrid on both surfaces, particularly the upper. The variety was introduced by the Gartons. It is of hybrid origin, Lincoln Red, Michigan Bronze and Waterloo being its parents.

Sunbrown (*T. vulgare*). Ears beardless, compact, square in section; glumes glabrous, red, keeled above, rounded below; grain red; stem stout, of medium length (4 feet), hollow; leaf rough on the upper surface.

White Monarch (*T. vulgare*). Ears beardless, medium lax, squarish in section; glumes glabrous, white, not strongly keeled; grain yellowish white; stem stout, medium length (4 feet or more), hollow; leaves scabrid above. This variety was raised by the Gartons from the following parents: Hunter's White, Victoria Red, and Rivet wheat.

Square Head's Master (*T. vulgare*). Ears beardless, compact, square in section; glumes glabrous, red, keeled above, rounded below; grain red; stem of medium length, stout. The variety is widely cultivated and may be found under many different names.

Rough Chaff (*T. vulgare*). Ears medium lax, beardless; glumes felted, yellowish-white in colour under favourable conditions, but liable to be stained during a wet season; grain amber-coloured. My plants frequently produce short awns on the paleæ of the terminal spikelets.

Golden Drop (*T. vulgare*). Ears medium lax, beardless; glumes glabrous, tinged with red; grain red.

Lammas (*T. vulgare*). Ears lax, beardless; glumes red; grain dark red.

Nursery (*T. vulgare*). Ears medium lax; chaff glabrous and red; grain red.

New Era (*T. vulgare*). Ears lax, bearded; glumes rounded below, glabrous; grain red. Of hybrid origin, introduced by the Gartons.

Stand-up White (*T. vulgare*). Ears compact, beardless; glumes rounded below, glabrous, white.

Standard Red. Similar to Square Head's Master.

"*Manitoba*" (*T. vulgare*). Manitoba wheat as received in this country is a mixture of a number of distinct varieties. The variety I have used under this name is lax, beardless; glumes white, grain red.

White Tuscan (*T. vulgare*), selected from a commercial sample which produced bearded and beardless plants. Ears lax, beardless; glumes white, grain white. Early ripening. It has never produced bearded plants on my plots.

"*Devon*" (*T. vulgare*). Variety unidentified but possibly Talavera de Bellevue[1]. Found amongst a crop of Old Hoary in Devonshire. Ears lax, beardless; glumes and grain white.

Hedgehog Wheat (syn. Hérisson, Club wheat, Igel; *T. compactum*). Ears dense, with spreading awns; glumes brownish-grey, glabrous; grain red; straw short and slender.

Polish Wheat (syn. Goose, Diamond wheat; *T. polonicum*). Ears lax, bearded; glumes unusually long (about 20 mm. or more), straw-coloured, glabrous; grain long, translucent, amber-coloured. The plants mature rapidly.

"Minnesota" (*T. durum*), an unnamed variety grown for macaroni-making in the United States. Ears compact, bearded; glumes keeled, reddish-grey; grain amber-coloured, translucent.

In addition to these a considerable number of other varieties have been used as parents, but another season must pass before the results can be recorded. Practically all of the characters used in classifying wheats are represented in the above varieties with the exception of the brittle rachis found among the varieties of *T. spelta*. Hybrids with this as one parent are now being raised.

Description of Hybrids (F_1).

Red King ♀ × *Rivet Wheat* ♂. Ears beardless, felted, lax, flattened to about the same extent as Red King; glumes grey, strongly keeled to the base; grain red to red-brown, silky at the apex, translucent; straw very long (6—7 feet), stout, hollow. Leaves broad and scabrid above. The striking vigour of the cross-bred is well exemplified in this case. Not only was the straw of unusual length but the tillering power was equally striking. This of course is largely dependent on the amount of space available for the plant, but grown under similar conditions to the parent plants (in this case 4½ inches from plant to plant and 6 between the rows), the hybrids had at least twice as many stems as the parents. Another noticeable peculiarity was that the lower spikelets, generally some two or three in number, were sterile. This is common in many of our varieties, including Red King, but as far as my experience goes

[1] Vilmorin, *Les meilleurs Blés*.

exceptional in Rivet. The reddish-brown colour of the grain of the hybrid is probably to be attributed to lack of sunshine during the ripening period[1]. The grey colour and also the felting of the glumes was less pronounced than in the parent Rivet wheat.

The reciprocal cross Rivet wheat ♀ × Red King ♂ was also made. After a careful examination of the two sets of hybrids I could find no difference between them.

Sunbrown ♀ × *Rivet* ♂. Ears beardless, compact, the internode length the same as that of Rivet wheat; glumes grey, strongly keeled to the base; grain reddish-brown. Stem stout, long (6—7 feet), hollow; leaves scabrid above.

The ears have therefore a general resemblance to those of the cross-bred Red King × Rivet. On comparing bunches of the two though, the former have a decidedly redder tinge than the latter.

White Monarch ♀ × *Rivet* ♂. Ears beardless, medium lax, squarish in section; glumes felted, grey, strongly keeled below; grain red, but a shade paler than that of Rivet wheat; stem stout, long (6 feet and over); leaf scabrid above. As in the preceding cross-breds, the extent of the felting was variable and might readily have been overlooked in some ears. One other character, occasionally of systematic value, shown in the cross-bred is the "spreading" of the spikelets. This occurs in Rivet wheat where the flowers lie widely apart, but not in White Monarch. The same habit was detected, though not so obviously, in the cross-bred Rivet × Red King.

Square Head's Master ♀ × *White Monarch* ♂. Beardless, lax and flattened; glumes glabrous, red, rounded below; grain red, translucent; stem long (5 feet and over), stout.

The red colouring of the glumes was not quite so intense as that of Square Head's Master[1].

The reciprocal cross White Monarch ♀ × Square Head's Master ♂ gave cross-breds identical in every respect.

Red King ♀ × *Standard Red* ♂. Ears medium lax, glumes red, grain red. The laxness of the ears is slightly greater than that of Red King (Plate I. fig. 2).

Rough Chaff ♀ × *Golden Drop* ♂. Ears medium lax; glumes felted, tinged with red; grain red.

Lammas ♀ × *Manitoba* ♂. Ears lax; glumes and grain red.

Rough Chaff ♀ × *Manitoba* ♂. Ears lax; glumes felted, white; grain red.

[1] That is in 1902. Both 1902 and 1903 were peculiarly bad seasons for work of this kind. They were too wet and sunless. 1904 on the other hand was excellent.

Nursery ♀ × *Rough Chaff* ♂. Ears medium lax; glumes felted, red; grain red.

New Era ♀ × *Square Head's Master* ♂. Ears medium lax; glumes red; grain red.

Red King ♀ × *Stand-up White* ♂. Ears medium lax; glumes white; grain red.

White Tuscan ♀ × *Preston* ♂. Ears lax, beardless; chaff tinged with red; grain red.

White Tuscan ♀ × *Manitoba* ♂. Ears lax; chaff white; grain red.

Devon ♀ × *Hedgehog Wheat* ♂. Ears compact, beardless; glumes brown; grain red and translucent; straw long (up to 5 feet), stout. In general appearance the hybrid resembles the variety Thickset or Hickling (Plate I. fig. 3).

Polish ♀ × *Rivet Wheat* ♂. Ears lax, bearded; glumes felted, varying in colour from pale grey to isabelline white, long but shorter than those of Polish wheat; grains long, but shorter than those of Polish wheat, red, translucent. The plants mature slowly.

The reciprocal cross-bred Rivet ♀ × Polish wheat ♂ was identical in appearance (Plate I. fig. 4).

The grain from selected ears of the cross-breds was sown early, as much of it was poor and shrivelled, partly owing to attacks of rust, partly to the lack of sunshine. Its germinating power was however satisfactory. Even in the seedling stage it became evident that "splitting" was occurring, for among the hybrids with Rivet wheat as one parent there were obviously different types of leaf shape and leaf colour. The vigour of the plants was also very variable, and by the time of ripening many of the weaker individuals had been crowded out of existence by their more vigorous neighbours. By then some of the plants were standing 7 feet high, while some few on the other hand were barely 18 inches. This dwarfing was not due to over-crowding, for several of these lowly plants grew on the open margin of the plots, and in one small plot containing three of them each had over a foot of clear space either side. The dwarf individuals only occurred on plots with a Rivet parentage. The period of maturation was again very variable, some few plants ripening their grain early in August, but the majority not until late in the month or the beginning of September. Taking the plants of this generation (F_2) as a whole they were not characterized by great fertility as in the preceding generation. About 10 per cent. of them were altogether sterile, and many produced only a small quantity of grain. There were a few noteworthy exceptions though; one plant, for instance, produced 1,280 grains.

DETAILED ACCOUNT OF THE VARIOUS CHARACTERS AND THEIR BEHAVIOUR IN F_1 AND F_2.

BEARDLESS × BEARDED.

The beardless condition is a dominant, the bearded a recessive character. This result has already been obtained by numerous workers. Rimpau's crosses between Red German bearded wheat and Kessingland, Rivet wheat and Saxon Red wheat, and White Spelt and Red German bearded wheat, were all beardless in the first generation[1].

Further, Spillman[2] and Tschermak[3] have obtained similar results in the first generation and also shown that in the second generation the beardless and bearded plants occur in the usual Mendelian ratio of 3 : 1.

One peculiar case has to be recorded. Vilmorin[4] crossed *Triticum polonicum* and Pétanielle blanche (a white Rivet-like wheat), both of which are bearded, and obtained a beardless hybrid. In this case then the combination of two characters which are recessive appeared to give a dominant. It seems probable though that the hybrid was really bearded, but the awns were shed on ripening. This phenomenon is not unusual and I have met with it in the very similar cross-bred Polish × Rivet wheat.

The following hybrids were without exception beardless: Rivet × Red King, Sunbrown × Rivet, White Monarch × Rivet, Rivet × Red King, Bearded White × Stand-up White, Devon × Hedgehog. The next generation (F_2) consisted of beardless and bearded plants. Out of one total of 364 plants 91 were bearded and 273 beardless; in another case 60 were bearded and 27 beardless; in another 34 and 11; in another 58 and 16; in another 15 and 4. Taking all the plots together this gives 440 beardless to 149 bearded, or a ratio of 2·95 : 1, a sufficiently near approximation to the expected ratio of 3 : 1.

Among this number were a few plants with the short terminal awns, up to half an inch in length. As this occurs in the awnless parents such plants were reckoned with the beardless forms. In the succeeding generation F_3 the bearded forms, *i.e.* the recessives, without exception bred true, whilst the beardless forms either bred true, *i.e.* pure dominants, or gave a mixture of bearded and beardless plants. A statistical

[1] Rimpau, *loc. cit.* [2] *Science*, 1902, Vol. XVI. p. 794.

[3] Tschermak, *loc. cit.*

[4] Vilmorin, *Bull. Soc. Bot. France*, T. XXXV. p. 49, 1888. See also T. XXVII. p. 73 and p. 356, 1880.

examination of two of such plots from Rivet × Red King gave a total of 94 beardless to 32 bearded plants. Among a total number of 163 plots from this cross (F_3) 88 produced a mixed offspring, corresponding to the $2DR$ of $D - 2DR - R$ in F_2. The numbers are a little wide of the expected ratio 2 : 1, but owing to the small number of plants which survived the winter (1903) one could not always be certain that a plot with say only half-a-dozen beardless plants represented a pure extracted dominant or a hybrid, for with so small a number the bearded (recessive) forms might well have been missing.

Velvet Chaff × Glabrous Chaff.

The felted or velvety character is dominant, the glabrous recessive.

This is deducible from Rimpau's crosses between Rivet and Square Head wheat, Mainstay and Square Head, Early Red American and Mainstay, and from a number of natural crosses which he has recorded. Vilmorin has obtained similar results in the case of a Spelt crossed with Blé à duvet (Rough Chaff), and Spillman and Tschermak have again proved that in the second generation three velvet chaffed wheats are produced to each smooth chaffed plant.

Nevertheless some difficulties occur on a further examination of this pair of characters. Thus Rimpau's cross between Saxon wheat (glabrous) and Rivet wheat (velvet) is quoted by de Vries[1] as an example of a character usually recessive being dominant.

On referring to the original the hybrid is found to be described as "vollig der Vaterpflanze" (*i.e.* Saxon Red). No special mention is made of any particular character and further no hairs can be distinguished in the figure of it (Taf. XIII. Nr. 13). Rimpau also makes no mention of the felted character in the hybrids resulting from the union of Rivet and Red German Bearded wheat, though in the case of Red American × Mainstay he describes the felting as being slight but distinct.

In the following hybrids the glumes were felted:—Rivet × Red King, Sunbrown × Rivet, White Monarch × Rivet, Red King × Rivet, Rough Chaff × Golden Drop, Rough Chaff × Nursery, Manitoba × Rough Chaff, Polish × Rivet. On comparing them though there was found to be this difference. In those with Rivet parentage the felting was very variable in extent, but where Rough Chaff was one parent

[1] De Vries, *Mutationstheorie*, Band II. p. 40.

it was constant and as fully marked as in that parent. None of the Rivet cross-breds were as strongly felted as the Rivet itself, and many would have been classed as glabrous unless they had been examined under a lens.

Perfectly glabrous ears did not occur. The gradation from felted ears to glabrous was so gradual that it was impossible to divide the series into strongly and slightly felted individuals.

An examination of my stock of Rivet wheat showed that this particular character was a singularly constant one, so that no explanation could be found by assuming parental variation.

The case then is obviously different from any of those met with by Mendel in peas. If the characters are represented as *I* and *II*, and the hybrid by *a*, a diagram such as:—

a

I ———————————————————— *II*

would represent the character *I* as being regularly dominant, while such a case as the above would have to be represented as:—

$a \ a^1 \ a^2 \ a^3 \ a^4 \ a^5 \ a^6 \ a^7 \ a^8$

I ———————————————————— *II*

the individuals nearest *I* being strongly hairy.

I am inclined to think that Rimpau's hybrids would be included in this second group, and then it would be quite intelligible that the slight hairiness, say of a^7 or a^8, should have escaped notice, particularly as at that time no special attention had been called to the necessity of examining the hybrids character by character.

In the next generation (F_2) felted and glabrous individuals occur:—Rough Chaff × Golden Drop, 63 felted to 23 glabrous; Manitoba × Rough Chaff, 373 : 140; Rough Chaff × Nursery, 262 : 79. The totals for these three plots therefore give the ratio of 698 : 242, or approximately 3 : 1.

In the cases where Rivet wheat was one parent the following figures were obtained:—Rivet × White Monarch, 23 : 17; Sunbrown × Rivet, 49 : 22; Red King × Rivet, 151 : 77; or a total ratio of 223 : 116[1].

The separation was variable where Rivet wheat was the felted parent, for plants occurred with ears which were strongly felted

[1] The figures for Polish × Rivet and its reciprocal have not been ascertained yet.

whilst others were almost glabrous, together with all possible intermediates between these extremes. The number of individuals examined, namely 339, should be sufficient to have given a reliable estimate of the proportions of felted and smooth individuals. The ratio obtained (223 : 116) is strongly suggestive of a ratio of 2 : 1.

However, a further examination of the next generation (F_3) pointed conclusively to the fact that the segregation of this pair of characters occurred according to the usual 3 : 1 ratio. Thus among the plots of Rivet × Red King (F_3) were some with the following ratios of felted to smooth :—66 : 22, 38 : 13, 8 : 2, 18 : 9, 84 : 29, or a total of 214 : 75.

It is possible that an explanation of this wide departure from the normal ratio in the first generation from the Rivet hybrids may be found in a partial shedding of the hairs on the glumes during ripening. The matter is being further investigated.

Grey and White Chaff.

The grey colour of the glumes and paleæ is shown to be a dominant character in the descriptions of the hybrids with Rivet wheat. From the literature already in existence it was evident that difficulties would be met with on examining this particular pair of characters. Thus Rimpau's crosses between Rivet wheat and Red German Bearded and Square Head gave plants which were somewhat like Rivet wheat in colour, *i.e.* grey was dominant, but the cross between Rivet wheat and Saxon Red (p. 24) would again form an exception as it gave plants resembling Saxon Red.

I have examined over two hundred plants from the series (F_1) mentioned above, and have without exception been able to detect grey colouring, though in some cases it was only slightly developed.

In extreme cases it was almost as intense as in Rivet wheat, whilst in many on the other hand the general coloration of the ears much resembled that of the other parent. In the latter case the grey colouring was for the most part confined to the longitudinal strips in the glumes where it appears to be most intense in the Rivet wheat. The crosses with *Triticum polonicum* afford a typical case of this, for at first sight they resemble that parent in colour very markedly but on closer inspection the grey patches are visible.

Were the grey colour inherited in full intensity the hybrids with red and white chaffed parents should show precisely the same grey-coloured chaff in each case, but taking them in separate bundles one could say with certainty which was descended from a red-chaffed and which was descended from a white-chaffed wheat.

It is evident then that a pre-Mendelian description of such hybrids would frequently omit any mention of so poorly marked a character, but the more detailed examinations, character by character, which are now necessary would at once detect it. Rimpau's description of the hybrid between Rivet wheat and Saxon Red cannot then be considered as an exceptional case showing the grey colouring as a recessive character. It rather refers to a hybrid diagrammatically represented as a^6 in a series where I represents the irregularly dominant grey colour (cf. p. 25).

The explanation of this irregularity is probably to be found in the fact that the grey-colouring is a peculiarly variable character in the parent Rivet wheat.

In the second generation grey and white chaff separate out in the usual proportions. Thus from the plants produced from Red King × Rivet (F_2) 161 were grey and 56 white, or approximately three grey plants to one white (a number of discoloured individuals being excluded as doubtful). The most striking point with regard to this particular pair of characters in this generation was their extraordinary variability, the coloration ranging from almost black to isabelline white, a far greater range than could be found in the original Rivet wheat. In spite of this the cases where one could not be certain of the grey character were merely those due to accidental discoloration. The extremely dark plants often had the greater part of the upper internode coloured with purple.

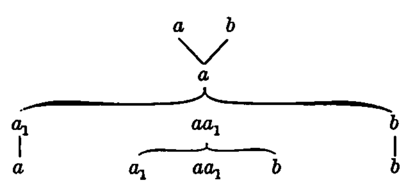
It seems probable that this increased range of variation, which also occurs with other characters besides the pair under consideration, will be of some use in the building-up of new wheats where it becomes necessary to strengthen or weaken them in any particular way. Fixed forms of these extreme dark and extreme light plants have been obtained in F_3.

In the first generation from the cross-bred Rivet × Polish wheat the grey coloration is practically wanting, and looking at the plots casually one would have said that a case of failure to segregate had occurred. A more detailed examination has shown that many of the glumes are faintly marked with grey, but no single plant out of some 2000 was as dark in colour as even a light ear of the parent Rivet.

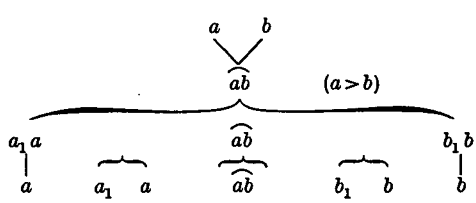
No figures can be given at present to show the relative frequency of the grey and white forms, as the examination of this particular set of plants has had to be deferred.

Red and White Chaff.

The fact that the red colour of the glumes is a dominant and the white a recessive character is evident from a considerable number of cases already known. A typical example is found in a cross made by Vilmorin between a white spelt and a red wheat which produced (F_1) a red spelt-like wheat. Spillman's experiments also point to dominance of red over white, but both Rimpau and Tschermak have described examples in which a mixing of the parental colours occurred. In the following hybrids the ears were red or reddish: Red King × Square Head's Master, Red King × Standard Red, White Monarch × Square Head's Master and its reciprocal, Rough Chaff × Golden Drop, Lammas × Manitoba, Devon × Hedgehog (brown). Where the full red colour was not developed the result is almost certainly to be explained by the lack of sunshine in 1902 and 1903, for in all the cross-breds grown in 1904 the colour was as clear and as well developed as in the parents. At the same time the possibility is not excluded that we again have to deal with irregular dominance similar to that shown by the grey colour. The difficulty is recognized by Tschermak, who concludes that this pair of characters does not show simple dominance and recessiveness. If Mendel's scheme is represented as



he represents the behaviour of this colour pair as:



the hybrid showing characters belonging to each parent, and subsequently splitting in a more complex fashion than those with strictly Mendelian characters.

To test this point several hundred plants of the F_2 generation of each of these red cross-breds were raised. In 1903 the season proved unfavourable and finally only those of Rough Chaff × Golden Drop were harvested. The ears from these plants were then compared with Golden Drop (the red parent) and Rough Chaff (the white parent) and, in spite of the fact that the former would be considered a very light coloured type of a red wheat, there was no difficulty in separating them out into 64 red and 21 white plants, that is, the usual 3 : 1 ratio. At the same time the red colour of the ears frequently differed from that of Golden Drop, sometimes being darker, sometimes lighter, but this variation was so frequently found among ears from one and the same plant that it was impossible to group them, as individuals, into plants showing the pure red and plants showing the intermediate colour.

One further test of the accuracy of this counting was possible by comparing the distribution of the red and white among the velvet and smooth chaffed wheats. Neglecting five plants which were poorly developed and stained, the remaining 81 were composed of 5 smooth white, 15 velvet white, 16 smooth red, and 45 velvet red individuals, that is, the expected distribution of:

$$9VR \quad 3VW \quad 3SR \quad 1SW.$$

In 1904, under far more favourable conditions, the F_2 generation of Lammas and Manitoba was raised. It consisted of 329 red individuals to 115 white. The red coloration was practically constant, and no intermediates occurred. It would seem therefore that the dominance of red over white is pure in these cases.

RED AND WHITE GRAIN.

The red colouring matter of the grain is confined to the testa of the seed and shows through the thin, transparent ovary wall. The white wheats do not possess this colouring matter, so red and white grains form an easily recognizable pair of characters. Imperfect ripening tends rather to exaggerate the difference, for the red grains are then usually liver-coloured, whilst the white grains become only a shade yellower. In the hybrid plants (F_1) of Rough Chaff × Golden Drop and Rivet × Polish wheat the grain was invariably of a clear red colour, so perfectly distinct from the amber colour (so-called "white") of Rough Chaff and Polish wheat, that a single grain could be picked out from a sample of them. In the next generation (F_2) the plants of Rough Chaff × Golden Drop were separated into red- and white-grained by matching them against the grain of their parents, Golden Drop and Rough Chaff. Six doubtful plants were neglected, leaving a total of 80; 60 of which had grain matching that of Golden Drop, 20 that of Rough Chaff. As a further test 200 ears taken from separate plants of Manitoba × Rough Chaff (F_2) were examined. They gave 154 red to 46 white-grained forms. Segregation into red and white grain also occurs in Rivet × Polish wheat (F_2) but no statistics are as yet available. There are also indications that dark red is dominant over light red, for the progeny of the cross-bred Lammas × Manitoba, the former of which has very dark grain, consists of dark and light grained individuals. The evidence therefore points to the fact that red is dominant over white and the splitting in F_2 is pure.

Keeled and Rounded Glumes.

This pair of differentiating characters occurs in the crosses between Rivet wheat with Red King, White Monarch and Sunbrown. In all cases the hybrids (F_1) showed the keeling of the glumes in undiminished intensity. In the following generation (F_2) keeled and rounded individuals occurred in the ratio of 171 : 58, 37 : 17, and 30 : 10. In F_3 one plot only, of Rivet × Sunbrown, was examined for this pair of characters. It contained 84 keeled and 26 rounded individuals. The totals are therefore 322 keeled to 111 rounded or a ratio of 3 : 1.

Lax and Dense Ears.

In practically all the varieties I have made use of there has been some slight difference in the length of the internodes between the spikelets, though the crosses between Rivet and Polish, and Devon and Hedgehog wheat are the only ones which afford a really well marked difference between the parents in this respect. Rimpau's[1] cross between early Red American and Square Head wheat, and Vilmorin's[2] between Polish wheat and Pétanielle blanche show that the lax type is dominant over the dense. In one set of Spillman's[3] crosses the length of the

[1] *loc. cit.* [2] *loc. cit.* [3] *loc. cit.*

hybrid ear is intermediate between that of the parents, and in the following generation lax, intermediate, and dense ears occur in the ratio of 1 : 2 : 1.

As a typical case we may take the cross between Square Head's Master and Red King with average internode lengths of 3·2 and 4·6 mms. respectively. The hybrid ears were laxer than the lax parent, averaging 4·8 mms. (Plate I. fig. 2).

The increased length of the hybrid ears is probably simply a correlation with the increased height of the hybrid plants, it being a general rule that dense ears are associated with a short straw, and lax ears with a long straw.

In the second generation (F_2) at the first sight it appeared as if the splitting into lax and dense ears was most irregular, owing to the fact that many of the plants produced long, dense ears, or long, lax ears, or the corresponding short forms. It was found impossible to sort the ears into the two types by inspection only, so a typical ear from each of one hundred individuals was measured, the number of spikelets counted and the average length of the internodes estimated. This gave a result of 78 lax to 22 dense individuals, 4·6 mms. and over being considered as lax and measurements below that as dense. The figures are suggestive of the three to one ratio though they depart rather too widely from it.

Among the lax-eared individuals the exaggeration of the character was frequently met with, 24 plants having an average internode length of over 4·6 mms., while one ear showed as high a figure as 5·0 mms. No ears were found with shorter internodes than the dense parent, though from inspection only it appeared that this would be the case.

In the case of Rivet wheat (3·6 mms.) × Polish wheat (6·6 mms.) the hybrid internodes averaged 5·8 mms. The F_2 generation consisted of plants with internode lengths ranging from 3·1 to 6·8 mms. A large number were measured by Mr W. L. Balls and the figures obtained point to a segregation into dense, intermediate, and lax in the ratio of 130 : 362 : 179 or (?) 1 : 2 : 1. The results stated are provisional, for the matter is still being investigated. The first generation of Devon × Hedgehog wheat has produced ears which are intermediate between their parents in respect to the lax and dense characters. It resembles therefore the hybrid described by Spillman which produced the lax, intermediate and dense ears in F_2[1]. The F_2 generation of this has still to be grown.

[1] Spillman, *loc. cit.*

Hollow and Solid Straw.

The cultivated varieties of *T. vulgare* show in all that I have examined a hollow straw while Rivet wheat (*T. turgidum*) has a thin straw, especially below the ear, which is practically filled with pith—a fact well known to Jethro Tull, who describes it as "having its straw full of pith like a rush." The two types are so distinct that one often hears the Rivet straw described as "goose-necked" by agriculturists.

When wheats showing the two types are crossed the resultant hybrid always has a thick, hollow stem similar to that of the *T. vulgare* variety. Rimpau's illustrations do not show this particular pair of characters as the ears are cut off too closely, and I can find no reference to it in the literature I have consulted, though from the technical point of view straw structure is almost as important as yield of grain.

That the hollow type is dominant over the solid is however evident enough from an examination of the Rivet series of crosses.

In the following generation (F_2) splitting occurs and a number of very different types of straws occur, some being thick and solid, slender and solid, thick and hollow, thin and hollow, ribbed and ribless, rough and smooth. These were sorted out into hollow and solid individuals, with the result that 170 of the former were found to 56 of the latter. This pair of characters then splits in the usual Mendelian ratio.

A further examination of the straws gave a sufficient reason for the multitude of forms occurring in this generation, it being found that numbers of other characteristics could be detected.

These are best seen in transverse sections of the stems, taken for the sake of uniformity from the middle of the uppermost internode in each case. The two types are afforded by Rivet wheat and Red King. In the former the outline of the stem is strongly ridged, the ridges being formed by massive girders of sclerenchyma running out from the large innermost bundles. The parenchymatous tissue of the pith either completely or almost completely fills the innermost part of the sections. In Red King the stem outline is nearly circular, its regularity being only broken by slight undulations formed for the most part by sclerenchyma girders from the smaller vascular bundles. Girders are also formed from the larger innermost vascular bundles. The epidermis, particularly on the ridges, bears numbers of short, stiff bristles. The parenchyma of the pith forms a thin layer only, the stem being hollow. The sclerenchyma girders are far less massive throughout than those of Rivet wheat, and those from the innermost ring of bundles are no more developed than those from the smaller exterior bundles. Sections of the stem of the hybrid generation (F_1) are more strongly ridged than those of Red King owing to the greater development of sclerenchymatous tissue, the pith is only slightly developed, and the short, stiff epidermal hairs, absent in Rivet wheat, are present on the ridges.

The development of the girders is not, however, as marked as in Rivet wheat. Reciprocal crosses, and crosses between Rivet wheat and Sunbrown, show the same characters. From this it would appear that a hollow pith and solid pith, bristly and smooth epidermis, angular and circular stem sections, massive and slight sclerenchyma girders are differentiating pairs of characters, the first mentioned in each case being dominant. The last pair belongs to the "more or less" order, and the question might be raised as to whether the increased amount of sclerenchyma is not to be correlated with the increased vigour of the hybrids.

The numerous types of stem are, therefore, the expected result of shuffling a number of pairs of characters together. An anatomical examination of a number of chosen stems resulted in finding the majority of the predictable types, but the task of grouping the whole set statistically has still to be undertaken. The fact that the one pair so examined splits in a Mendelian ratio makes it probable that the remainder of these anatomical characteristics do so also.

The same types of splitting have also been observed among the heterozygotes (DR's) in F_2 and a number of the more promising forms have been saved to breed from later.

ROUGH AND SMOOTH FOLIAGE.

From the descriptions of the hybrids it is clear that the rough type of leaf is dominant over smooth. Sections of the leaves of Rivet wheat, the smooth parent, show that the upper surface in particular is covered with slender hairs. Similar hairs, though relatively less abundantly, occur on the leaves of Sunbrown, White Monarch, and Red King, but here they are mixed with short, stiff bristles, similar to those occurring on the stem. The presence of these bristles accounts for the roughness of their foliage. The foliage of the F_1 generation of Rivet, crossed with either Red King, Sunbrown, or White Monarch, invariably bore short, stiff bristles interspersed with the longer silky hairs, showing that here again their presence is a dominant character, their absence a recessive.

Broad and Narrow Leaf-shapes.

Where a wheat exhibiting markedly broad foliage is crossed with one possessing narrow leaves the hybrid bears the broad type of leaf, as is shown in the single cross of Red King and Rivet wheat, and its reciprocal. In the next generation (F_2) broad and narrow foliage occurs together with leaves difficult to place definitely in either class. The numerical relation of these classes was investigated in one case with the result that 57 individuals were grouped as broad, 67 as narrow, and 110 were neither one nor the other.

Assuming that these 110 individuals were normal, and that the foliage was fully developed—the plants were not crowded together—the figures suggest a ratio of 1 : 2 : 1.

Probably the leaf colour affords yet another pair of characters, some varieties being a deep bluish-green others a glaucous green. Indications of this have been seen in several cases, but the matter has not been investigated.

Time of Ripening (Late and Early).

The hybrids between Polish wheat and Rivet wheat afforded an example of this particular pair of characters. Polish wheat is tender, and to avoid danger from frosts it has to be sown in this country about the middle of March, it then grows rapidly, rushes through its flowering and ripening stages, and may be harvested by the first week in August Rivet wheat, on the contrary, is hardy, and when autumn sown is usually about the last of the commonly grown varieties in this country to ripen. On my plots during 1903 it did not ripen until the third week in August. Definite dates are difficult to give, because in thinly sown plots the plants tiller considerably, and the smaller ears of the side branches may be a fortnight later in ripening than the ears of the main branches.

The grains obtained as the result of the crosses made in 1902 were sown on March 15th in order to avoid the risk of damage by frost, as there was the possibility of tenderness being a dominant character, and a few grains of Polish and Rivet wheat were put in alongside to serve as controls. The Polish wheat showed signs of ripening early in August, and by the third week of the month the ears, even on the side tillers, were thoroughly matured. The hybrid plants, however, pushed their ears through the sheaths from five to seven days later, and produced no ripe grain until September 17th. The side tillers were not harvested until a month later, and even then they were not thoroughly ripened. The late sown Rivet wheat ripened the main ears on the plants late in September, but the ears of the side tillers were not ripe when the plots were finally cleared away on October 20th. The time of ripening for the hybrids is a little earlier than that of the late parent Rivet wheat.

In the next generation F_2 (sown Feb. 26th) all the plants flowered simultaneously; the ears pushed through the sheaths on June 11th, and the stamens were ripe on June 18th. The Polish wheat sown on the same date also flowered at this period, but the Rivet wheat was twelve days later. The first signs of ripening were noticed on July 10th. By July 30th many plants were ripe, others were almost ripe, others dead green. At this date the Polish wheat was ripe, whilst the Rivet was quite green.

A statistical examination was then made, the following being the criteria used for grouping the plants:—Ripe, glumes and straw yellow, grain hard; half-ripe, awns yellow, glumes beginning to turn yellow, straw yellowish-green, grain soft; unripe, green throughout. The results were 103 ripe, 210 half-ripe, 100 unripe. A second plot[1] gave 84 ripe, 171 half-ripe, 79 unripe. The figures clearly indicate a ratio of 1 : 2 : 1.

On August 3rd a small plot of 74 individuals, the survivors of 200 autumn-sown grains, contained 56 ripened plants and 18 unripe, so that an examination at this stage would have pointed to the fact that early ripening was a dominant character. The true state of affairs is of course shown by the other statistics. It is worth noting that the time of ripening was in no way correlated with the habits of the plants. Individuals resembling Polish wheat were either early, late, or intermediate in their ripening periods, and the same is true for the Rivet-like individuals.

Probably similar results could have been obtained with the other Rivet hybrids, though there was not so marked a difference in the ripening

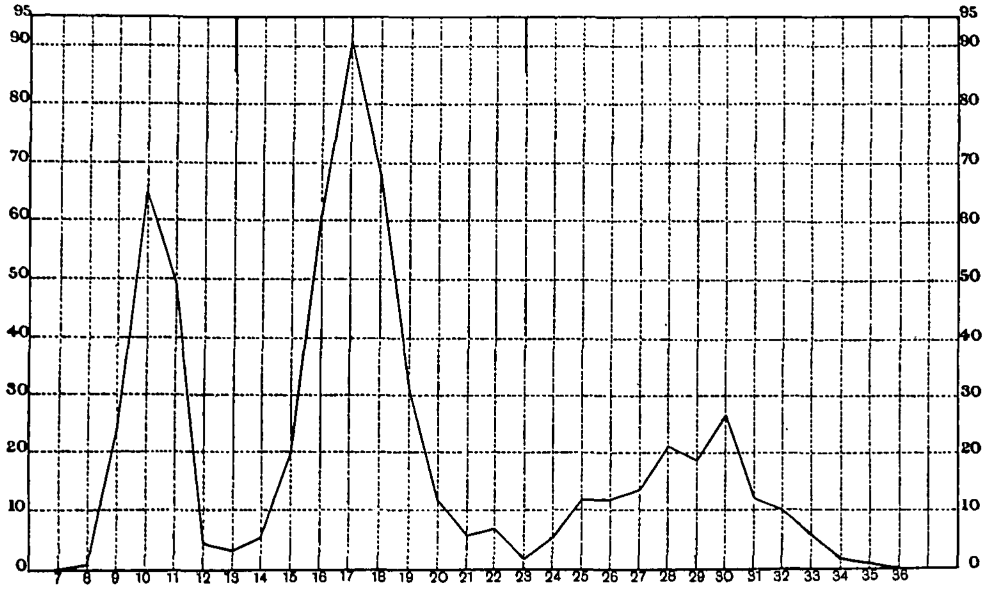
[1] W. L. B.

periods. In both the F_2 and F_3 generations of these hybrids great differences were observed between individuals in this respect. This season (1904), for instance, ripe ears were gathered on August 7th from Rivet × Red King (F_3), whilst other plants were not fully ripe at the end of the month. This points to an intensification of characters similar to that already described in the case of the grey colouring of the glumes. The case is of interest as it affords an example of a pair of constitutional as opposed to morphological characters.

Long and Short Glumes.

These characters are represented in the cross between Polish and Rivet wheat and its reciprocal. A somewhat similar cross was made by Vilmorin between Polish wheat and Pétanielle blanche, a variety of *T. durum*. The cross-bred (F_1) produced glumes which were intermediate in length between those of the parents. The same result occurred with my cross-breds, the glumes again being of an intermediate size in both cases. The average glume length of 21 plants was 17 mms., that of the parents 28 and 9 mms. respectively. The peculiar loose appearance of the ears of Polish wheat caused by the glumes standing away from the rachis in an irregular manner was not represented in the cross-breds. Their more compact manner of growth resulted in square ears more like those of Rivet wheat (Plate I. fig. 4).

The F_2 generation at first sight seemed to consist of individuals with glume lengths varying from one extreme to the other. The long, intermediate, and short types were obviously present, but one continually hesitated as to whether any particular individuals should be classed as short, or intermediate or long. The glume lengths of a number of plants were therefore measured with direct-reading callipers, the measurements being taken from the base to the shoulder of the glume. In each case the third glume from the base of the ear was taken to be the standard. This was considered necessary as the glumes of the spikelets towards the apex of the ear are smaller than those towards the base, and preliminary measurements pointed to this as the best position for giving representative results. The glume lengths ranged from 8 to 35 mms. These were plotted on squared paper, the lengths along the base line, the number of individuals vertically, with the result that the curve so obtained was found to be sharply divided into three distinct portions. The three separate curves corresponded with the small, the intermediate, and the large glumes. On counting the number of plants represented in each curve they were found to be 149, 304, and 142. A second series of measurements on the reciprocals gave the numbers 205, 432, 188. The figures are a fair approximation to the ratio of 1 : 2 : 1, showing that on the separation



Glume length curve of 595 individuals of Rivet × Polish wheat, F_2.

of the gametes of the hybrid into those carrying the long and short characters where long meets long we have the long type of glume, similarly where short meets short the short type, and where long meets short, as in the original operation of artificially crossing, the intermediate type is produced.

The curves are of interest from another point of view. That corresponding with the small glumed type is steep and shows a range of 5 mms. (from 8—13 mms.), that corresponding to the large type is flattened with a range of 12 mms. (from 23—35 mms.), whilst the intermediate curve is compounded of the flat and steep curves with a range of 10 mms. (from 13—23 mms.). The steep and flat curves correspond broadly with those of the parents. Curves plotted with the glume lengths of Rivet wheat are steep, those with the glume length of Polish wheat flat, for in this sub-species the glume length varies over a considerable range. No detailed figures are given here as the matter is one which is worth further investigation.

Long and Short Grains.

These characters have also been examined in the Polish × Rivet wheat hybrids and their offspring. In my material the grain lengths are 10·1 and 7·2 mms. respectively. Before describing the results it is necessary to have a clear idea of the structure of a grain of wheat. It must be realized that we are dealing with a fruit in which the carpel wall is fused with the testa of the seed proper in such a manner that the seed cannot be separated from it. The study of the grain characters is further complicated by the fact that the endosperm of a grain resulting from an artificial cross is as much a hybrid as the embryo itself, for this endosperm arises from the definitive nucleus which has previously been fertilized by one of the two generative nuclei of the pollen tube. The grain resulting from a cross is therefore partly hybrid (the endosperm and embryo) and partly a portion of the female parent (the testa and carpel wall), or to put the matter crudely the endosperm is a generation ahead of the grain coats[1]. Presumably the shape of the grain is determined by the endosperm.

The hybrid grains of the reciprocal crosses were, as is usually the case, slightly shrivelled, but the shapes and colours corresponded with those of the female parents, those borne on the Polish parent being longer and more slender in shape than those on the Rivet parent and also paler in colour. In the following generation (F_1 of the plants) the grains produced by the reciprocal crosses were identical in appearance. They were relatively broader than those of Polish wheat and longer than those of Rivet wheat—the length being on the average 9·0 mms. Such grains could properly be described as intermediate between those of the parents. There was no segregation into the long and short types in this generation (Plate I. fig. 5).

The generation raised from these grains (F_2 of the plants, F_3 of the endosperm) consisted of individuals with short, intermediate, and long grains. The distribution of these will have to be considered later when I have found an opportunity to work through the whole crop. It may however be stated that the small grains only occur among the plants with small glumes, the large grains among the plants with large glumes[2].

[1] No actual proof of this has been given in the case of wheat, but Guignard has shown that this double fertilization occurs in maize.

[2] Some 200 individuals examined.

Similar cases though not sufficiently distinct for accurate estimation have occurred in the crosses between Rivet and Red King and a variety of *T. durum*.

This failure to segregate in the expected generation appears to afford a parallel to the case of the indent peas quoted by Tschermak and again investigated by Bateson[1]. No satisfactory explanation of the phenomena can be afforded, but when one takes into account the distribution of the different types of grain mentioned above it seems clear that the maternal plant characters—in this case of size of the glumes—in some way directly influence the seed characters in each generation.

HARD AND SOFT ENDOSPERMS.

I have used these terms in describing endosperm characters which really represent relatively high and low total nitrogen contents respectively, as the texture in itself affords a ready approximate method of judging this particular character. I recognize that the method is not an infallible one, but it is the best we have at present. The hard endosperms are usually translucent and glutenous, the soft ones opaque and starchy. Polish and Rivet wheat are examples of these two types. The endosperm of the grains produced as the actual result of the cross was hard in both sets of crosses. No stress can be laid on this fact though, as the ripening was not normal, the grains being shrivelled, and shrivelled grain is generally of this texture. The grain of the next generation (F_1 plants with F_2 endosperm) was all hard, whilst that of the parents ripened alongside as controls was hard in the case of Polish and soft in the case of Rivet wheat. Here and there a grain which was partially opaque (starchy) in patches occurred, but these were altogether confined to late-ripening side tillers. The number of such grains was not determined, but it was certainly less than 1 per cent. Their occurrence may safely be neglected, for grain from the side tillers of Polish wheat showed the same appearance. The expected segregation into hard and soft grain did not occur in this generation, but it occurs in the F_3 generation (F_2 of the plants), enough of which has been examined for me to be sure of this fact, but not enough to afford any statistics as to the numerical relationships existing between the two classes. A preliminary examination of the nitrogen contents as

[1] Presidential Address, Zoological Section, British Association Meeting, 1904.

determined by Kjeldahl's method, has given the following results. Polish wheat 2·3—2·5 °/₀ N.; Rivet wheat 1·8 °/₀ N.; hybrids 2·45, 2·3, 2·16, 2·04, 2·01, 2·0, 1·99, 1·94, 1·84, 1·83, 1·81, and 1·72. The figures are too small to base any conclusions on, but they seem to point to a segregation into high, intermediate, and low nitrogen contents. That segregation does occur is illustrated by the following fact. I sent two samples of the grain from an F_2 generation of a cross, in which these particular characters were not so distinct as in the case under consideration, to Mr A. E. Humphries, of Coxe's Lock Mill, for his opinion on them. Their parentage was not stated, yet he came to the conclusion that the grains were samples, not from cross-breds, but from the two original parents which he named[1]. Further evidence hardly seems necessary. 200 ears taken at random gave 152 hard to 48 soft-endospermed forms, or a ratio of 3 : 1.

IMMUNITY AND SUSCEPTIBILITY TO THE ATTACKS OF YELLOW RUST.

It is generally recognized that certain varieties of wheat are far more susceptible to the attacks of rust (as a rule *Puccinia glumarum*) than others, and from time to time suggestions have been made that more immune varieties should be sought for in order to minimize the losses annually caused by the attacks of this fungus[2]. Our knowledge of what determines immunity to the attacks of fungi is so slight that practically nothing has so far been achieved in this direction. One had no ideas of the lines on which such investigations should proceed. Some years of experience with numerous varieties not only of wheats but of barleys, swedes and potatoes have convinced me that these varieties can be grouped into classes according to their capacity for resisting various diseases, and that broadly speaking the grouping for one season holds with reasonable accuracy for other seasons, whether the disease is epidemic or only slight[3]. This being the case it follows that some varieties inherit a constitution making them capable of withstanding the attacks of certain fungi, others one making them susceptible. Other

[1] The difference between these types of endosperm is too subtle for me to attempt to describe. They are the slight differences which can only be appreciated by those who continually handle grain.

[2] As far back as 1815, Thomas Andrew Knight suggested that varieties proof against the mildew (or rust) should be raised. *Pamphleteer*, Vol. VI. p. 402.

[3] Cf. Eriksson, *Die Getreideroste*.

workers have come to the same conclusions. Thus Farrer states that the susceptibility to rust is hereditary in wheat[1]. If this is the case it is important to know what would happen when immune and susceptible varieties are crossed. To test this point Michigan Bronze was crossed with Rivet wheat and *vice versâ*. This latter wheat is as a rule fairly immune to yellow rust, and I used a strain selected two years previously (in 1899) which was peculiarly so. Michigan Bronze is probably the most susceptible wheat to yellow rust in existence. So badly are the plants attacked on my plots that I can hardly obtain enough grain each season to sow again.

Six plants of this parentage were raised. They were at first strong and vigorous, but by the middle of June (1902) the whole of their leaf surface was covered with rust pustules, which spread until the glumes and even the awns were orange with it. There was nothing to choose between the reciprocals in this respect either. On harvesting, these plants produced three grains which failed to germinate—a fact which will indicate the severity of the attack. A second series of crosses, those between Red King and Rivet wheat and the reciprocal, were examined from the same point of view. Red King is again very susceptible to yellow rust, possibly because Michigan Bronze is one of its parents. These hybrids were also badly rusted and indistinguishable in this respect from Red King growing alongside. They yielded, however, some 300 grains from which 260 plants were raised in 1903.

The season was favourable for such work, the rust epidemic being even worse than in the preceding year. It appeared as early as March 16th, but only spread slowly until the last week in May. By June 15th the epidemic was judged to be at its climax and the extent and percentage of disease were observed. The result was 78 plants almost free from disease, 118 showing a few pustules only, and 64 badly diseased. The extent of infection though increased steadily, and a second count on June 29th reduced the number of relatively immune plants to 64, whilst the remaining 195 were infected, for the most part badly. Now the ratio 64 : 195 seems to be too close an approximation to the ratio 1 : 3 to be a mere accident, and taken in conjunction with the fact that the F_1 generation was so badly attacked it is fair proof that susceptibility and immunity are definite Mendelian characters, the former being the dominant one.

This experiment has an important bearing on the "mycoplasm"

[1] Farrer, *Agric. Gazette of New South Wales*, 1889, Vol. IX. p. 131.

hypothesis put forward by Eriksson to account for certain facts with regard to epidemics of rust which need not be described in detail[1].

The main point of the hypothesis is that "a latent germ of disease is inherited from the parent plant," the parent being the *mother plant.* For a time this germ exists in "une symbiose intime" with the host plant, then under certain more or less defined external conditions the fungus protoplasm develops, giving rise to the parasitic rust.

This hypothesis is difficult to accept and still more difficult to disprove[2]. It was not until Eriksson actually demonstrated the "mycoplasm" and mycelium arising from it that this became possible. Then an elaborate histological examination carried out by Marshall Ward[3] showed clearly that what Eriksson had taken to be the developing fungus protoplasm consisted in reality of the haustoria pushed into the host-cells by the intercellular mycelium of the rust. Eriksson working in collaboration with Tischler[4] after further research admits the identity of his first "mycoplasm" with the haustoria, but now states that the granular contents of certain otherwise normal cells in the leaf of the wheat are the symbiotic blend of fungus and host-protoplasm[5].

Assuming then the truth of this hypothesis, and excluding for the time being all chance of external infection, the plants are immune if they inherit no "latent germs," and susceptible if they do so. Where external infection is possible the fact is not altered that immune plants inherit none since no disease occurs. If then A is immune and B is susceptible, A ♀ × B ♂ should be immune and B ♀ × A ♂ should be susceptible, since the "latent germs" are transmissible by the maternal parent[5]. The reciprocal crosses where Rivet wheat is the immune parent and Michigan Bronze or Red King the susceptible parent show however that this is not the case, for A ♀ × B ♂ and B ♀ × A ♂ are both highly susceptible. Here again then the "mycoplasm" hypothesis does not conform with the facts observed, but breaks down precisely where the student of heredity would expect it to. To bring it into conformity with our present knowledge of the subject it would have to be assumed that the "latent germs" can be handed on by the male parent as well, that is by way of the generative nuclei!

[1] Eriksson, *Ann. d. Sc. Nat.* T. XIV. p. 107, 1901.

[2] For negative evidence see Klebahn, *Die wirtswechselnden Röstpilze*, p. 79, 1904.

[3] Marshall Ward, *Proc. Roy. Soc.* Vol. LXXI. p. 353, 1903, and *Phil. Trans.* Vol. CXCVI. p. 29, 1903.

[4] Eriksson, *Comptes Rendus*, 1903. Cf. *Archiv für Botanik*, Band I, p. 143, 1903.

[5] *Ibid.* and *Rev. gén. de Bot.* 1898, T. X. p. 44.

This conception of immunity and susceptibility as definite constitutional characters throws some light on other aspects of the immunity problem. The most important of these is its bearing on the attempts to correlate immunity with morphological characters. By way of an example, one not infrequently finds it stated that thick-cuticled wheats or potatoes are more immune than those with thin cuticles. Where serious attempts have been made to trace any connection between such characters and immunity, as in the case of Marshall Ward's work on the Bromes[1], none whatever can be found, and one is driven to conclude that the differences are intraprotoplasmic. Now certain well-marked differences between the leaf characters of the varieties experimented with have already been pointed out, and at first sight it might well have been that immunity was dependent on one of these[2]. Nevertheless among the progeny of the hybrids (the F_2 generation) it was found that immunity by no means depended on any of these characters, leaves of the Red King type being as free from disease as those of the parent Rivet, whilst leaves of the Rivet type were as frequently badly rusted. The immunity simply depended on the luck of the shuffle.

The F_3 generation has in its turn given results which confirm those of the preceding generation. From the 260 plants composing it 163 plots were raised in 1904. One hundred and eighty-five were sown originally, but the conditions at seed-time were far from suitable and 21 failed entirely. Many plots only contained a few plants. At the end of May it became obvious that the relatively immune plants of the former season (*i.e.* the recessives) were breeding true in this respect, for each plot stood out sharply as a green patch among the orange plots of badly rusted individuals (dominants and hybrids). On counting out the plots 49 were relatively free from rust, and 114 were either rusty or contained an excess of rusty individuals. The separation into plots representing the extracted dominants and the mixed individuals was not attempted owing to the small number of plants on some of the plots, which would probably have led to confusion. The figures are very wide of the expected ratio, but the error is on the right side, for it is only reasonable to assume that the mortality would be greatest among the progeny of the most susceptible individuals in F_2 which in consequence of disease had produced seed of poor vitality. The failures should then be reckoned

[1] Marshall Ward, *Anns. Bot.* Vol. XVI. p. 233, 1902.

[2] Cf. Hartig's *Diseases of Trees*, Engl. edit. 1894, p. 171, where the cultivation of a woolly-leafed willow hybrid is recommended in place of its glabrous-leafed parent in districts where *Melampsora hartigii* is abundant.

with the badly rusted plots, which raises the number to 136 and gives a ratio of 136 : 49 or 2·8 : 1.

A further examination of four of the plots containing both classes of individuals gave 149 rusty to 48 relatively rust-free or a ratio of 3·1 : 1, figures which again agree with one's expectation on the assumption that the liability is dominant over immunity.

Further experiments are now being carried out with a more immune wheat than Rivet, which I have only recently obtained.

THICK AND THIN GLUMES.

This particular pair of characters has not been specially investigated. I was struck by the fact, while rubbing out the ears of the F_2 generations of crosses with Rivet parentage, that many shed their grain readily whilst in others the grain was so tightly gripped in the florets by thick outer glumes that it was difficult to remove the grain on rubbing. Extreme cases were met with in which the spikelets remained altogether closed and on rubbing the rachis broke into fragments. An examination of the parents then showed that the Rivet wheat had thicker glumes than the other varieties, a fact which had escaped my notice earlier. These plants with closed spikelets and brittle axes had for the most part lax ears, but the corresponding compact forms were present. The one point of interest associated with them is that the closed spikelet and brittle rachis are the distinguishing characteristics of *T. spelta*. As a matter of fact the plants were so spelt-like that several people with a special knowledge of wheats have had no hesitation in referring them to this sub-species. Further, practically all of the commoner types of spelts were represented among the thirty individuals occurring in Red King × Rivet (F_2), and the smaller number in Rivet × White Monarch. There were beardless, bearded, grey, red, and white varieties (Plate I. fig. 6).

Six years ago this would have been a striking demonstration of "reversion" to a more primitive type. Now one has become somewhat suspicious of these reversions and one examines them more critically than hitherto. In the first case we have no evidence which conclusively shows that *T. spelta* is a primitive type. It has probably been considered as such, solely on account of this habit of breaking the rachis for "seed" dispersal, which is common in many of the wild grasses. Further than this I see no possibility of advancing in this direction.

One other possibility had to be considered. Red King and White Monarch are already complex varieties raised by the Gartons and it might have been that spelt wheats were used in building them up, which in some way or other had split off again. Mr John Garton has kindly given me their pedigree, which contains no spelt parentage[1].

Such considerations as these led me to take the view that these individuals were spelt-like but not true spelts, that they had originated simply as the result of a fresh combination of characters represented in the parents, the thickness of the glumes having been intensified just as the grey colouring has been shown to be. In support of this view it has to be mentioned that individuals occurred among the non-spelt-like forms which had thinner glumes than those of the thin-glumed parents, that is an intensification of the thin character. If the glumes increase in thickness then it becomes more difficult for the developing ovaries to push them open, and a point is reached at which the spikelets remain closed. Such intermediate stages do occur. The spelt-like appearance of the ear would thus be accounted for. The brittleness of the rachis is more difficult to explain, for it would seem that a fresh character, one not found in either parent, has appeared. Here again though difficulties arise, for one finds individuals in which the rachis is only slightly brittle, others in which it is more brittle, so that the new character has made its appearance in a series of steps, not outright. On the whole it seems to me most probable that brittleness is a character correlated with closed spikelets, as "seed" dispersal would be impossible without it. Since harvesting the F_2 generation in 1903 I have carefully compared these spelt-like ears with the corresponding varieties of *T. spelta*, and I have been still further struck by their similarity in general appearance. At the same time, whilst admitting that from a systematist's point of view they may be identical, they are not so to one who is accustomed to the more minute distinctions between varieties met with in agricultural practice. The two points of difference which appeal to me most are: (1) that the texture of the grain is that of our English varieties—it would not yield the fine pastry-flour so characteristic of spelts; and (2) the rachis of the true spelt is more brittle than that of the spelt-like ears among the Rivet crosses. The F_3 generation of these spelt-like wheats showed the same types of segregation as the other hybrid forms. The bearded, white individuals (*i.e.* recessive in

[1] It is perhaps worth pointing out here that in spite of the complexity of the parentage of these two varieties they are indistinguishable from pure varieties even on further crossing—a fact Mendel's work would lead one to expect.

both characters) bred true, the beardless either bred true or threw bearded and beardless individuals, the velvet-chaffed either bred true or threw velvet and glabrous, and so on, but the closed spikelets and brittle rachis were retained in each case.

General Conclusions.

Summing up the results obtained up to the present we find that for each pair of unit characters segregation occurs in such a way that the results obtained agree with those expected on the assumption that the gametes are pure with respect to the characters they carry. The characters either separate out in the F_2 generation (or in the case of certain seed characters in the F_3 generation) according to the usual ratio of $3D:1R$, when one of the pair is dominant and the other recessive, or when the dominance is imperfect as in the case of grey over white glumes, or in the ratio of two intermediates to one of each of the pair where neither character can be considered as dominant over the other.

These characters may be grouped as follows:

A. Those showing pure dominance and thus resembling those described in peas by Mendel:

Dominant	Recessive
Beardless ears.	Bearded ears.
Felted[1] glumes.	Smooth glumes.
Keeled glumes.	Round glumes.
Lax ears.	Compact ears.
Red chaff.	White chaff.
Red grain.	White grain.
Thick and hollow stem.	Thin and solid stem.
Rough leaf surface.	Smooth leaf surface.
Bristles on stem.	Smooth stem.
Large sclerenchyma girders associated with an angular stem outline.	Small sclerenchyma girders and an almost circular outline.
Hard, translucent endosperm.	Soft, opaque endosperm.
Susceptibility to the attacks of Yellow Rust.	Immunity to Yellow Rust.

Where investigated in detail the ratio of $3D:1R$ has been found in F_2 for these pairs of characters.

[1] Where Rough Chaff is the felted parent.

B. Those showing irregular dominance; in F_1 some individuals show one of the pair in almost full intensity, but in others it may be hardly visible:

Felted glumes[1].	Glabrous glumes.
Grey colour of the glumes.	Red or white glumes.

In the F_2 the segregation is normal as in the preceding group.

C. Those in which there is no dominance of either character and the F_1 is intermediate between the parents in respect to the following pairs:

Lax and dense ears.
Large glumes and small glumes.
Long grains and short grains.
Early and late habit of ripening.

On segregation two of the intermediates occur to each of the pure characters, a ratio corresponding to $D : 2DR : R$.

Mendel's laws of inheritance apply to morphological, histological, and constitutional characters, and one can probably recognize as many pairs of characters as there are minute differences between the varieties experimented with. The various shades of red in the grain, the various degrees of laxness of the ears, etc., are each represented by character units.

No indisputable case of "reversion" has occurred. Where hybrid varieties of known parentage are crossed with other varieties no indications of the parentage of these hybrid varieties, excepting the characters they themselves show, have been met with.

Any desired combination of the characters represented in any two varieties can be obtained "fixed" in the first or at the most the second generation from the hybrids.

In addition to the characters described above a number of others dealing with fertility, hardiness, differences in the aleurone layer, etc. are being investigated.

I take this opportunity of acknowledging much kindly assistance given me whilst this work was in progress; in the first place by my wife, who carried out much of the preliminary work of hybridizing and aided me in sorting out each generation and recording the characters of the individual plants; and also to Mr A. E. Humphries, who besides

[1] Where Rivet wheat is the felted parent.

providing me with many varieties has given me much valuable advice whilst dealing with the endosperm characters and other more technical matters with which I am not particularly familiar.

EXPLANATION OF PLATE I.

Fig. 1. (*a*) Stand-up White, (*b*) Bearded White, (*c*) the hybrid (F_1) Stand-up White × Bearded White, showing that the beardless condition is dominant over the bearded.

Fig. 2. (*a*) Red King, (*b*) Standard Red, (*c*) Red King × Standard Red. The hybrid (F_1) is lax eared, and the internode length slightly exceeds that of the lax parent Red King.

Fig. 3. (*a*) Hedgehog, (*b*) Devon, (*c*) the hybrid Devon × Hedgehog, this is intermediate between the parents in respect to the laxness of the ear. Note the short awns at the apex of the spike. They occur, not infrequently, in Devon wheat.

Fig. 4. (*a*) Rivet, (*b*) Polish, (*c*) the hybrid Rivet × Polish. It is intermediate in laxness and glume length between its parents.

(a'), (a^2) dense and lax small glumed types of F_2,
(b'), (b^2) dense and lax large glumed types of F_2,
(c'), (c^2) dense and lax intermediate glumed types of F_2.
In (b') the awns have shed partially.

Fig. 5. Grains (*a*) of Rivet, (*b*) of Polish, (*c*) of the hybrid Polish × Rivet, F_1 plant generation.

Fig. 6. Beardless, spelt-like wheats showing the keeled glumes and closed spikelets. They are white, red or grey in colour.

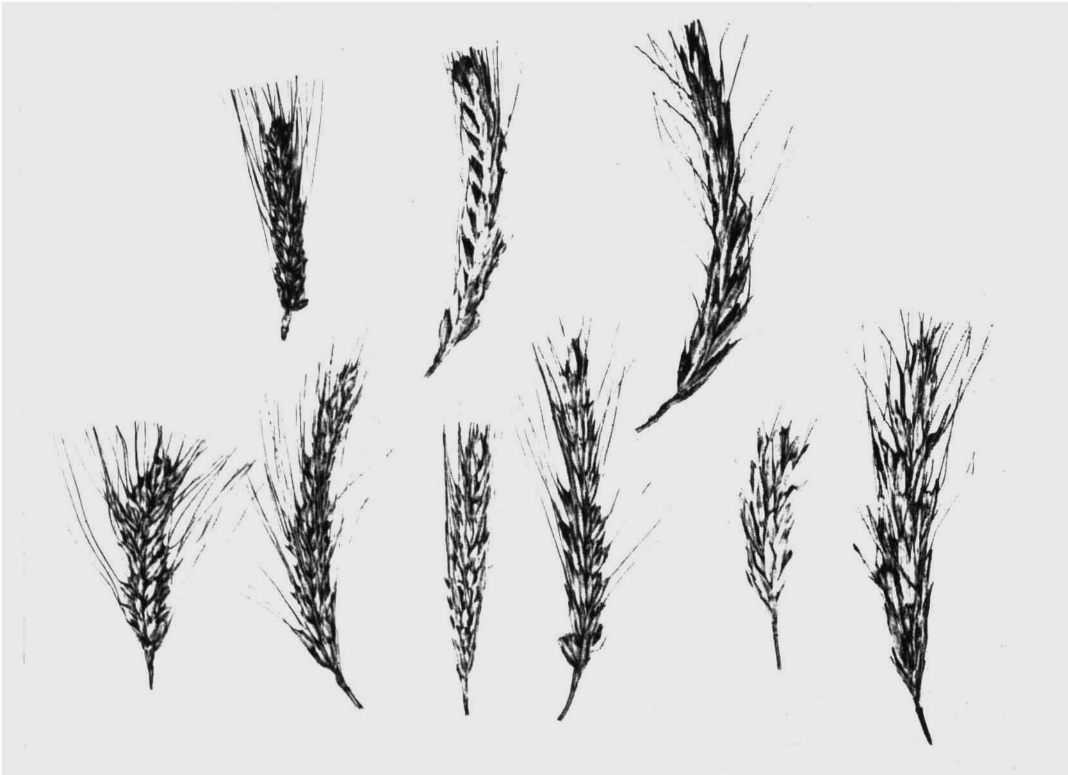
Fig. 1.

Fig. 2.

a *c* *b*

Fig. 3.

a *c* *b*



a' *a²* *c'* *c²* *b'* *b²*

Fig. 4.

Fig. 5. Fig. 6.

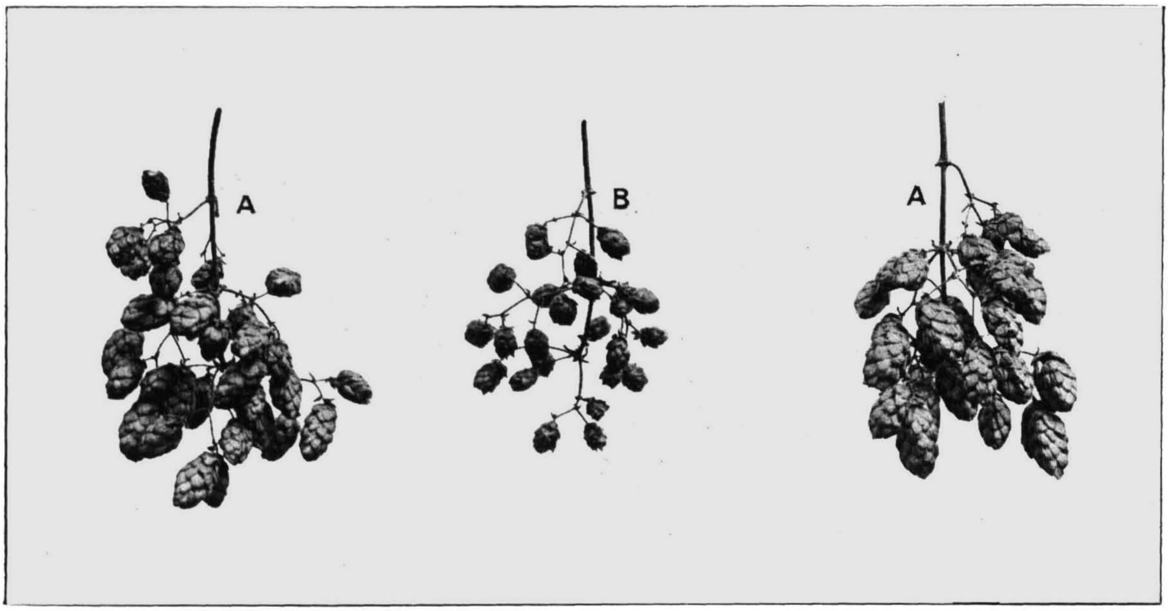


Fig. 2.—Seed and Seedless Colegate's Hops.

A.—Seed hops (pollinated). B.—Seedless hops (control—not pollinated).

Photographed 42 days after pollination.

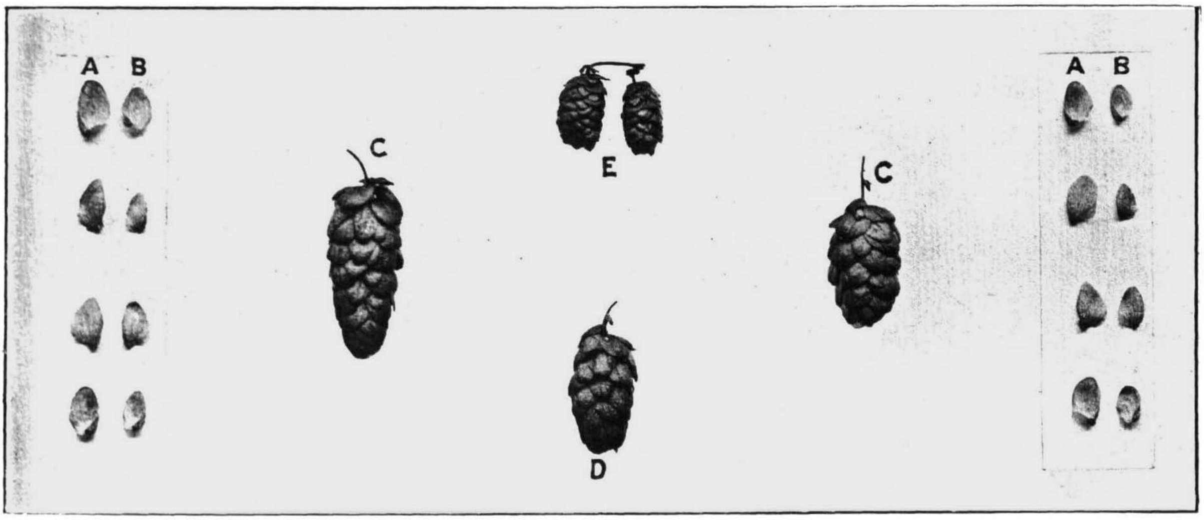


Fig. 3.—Seed and Seedless Hops and Bracteoles.

A.—Bracteoles with perfect seeds. C.—Seed hops (naturally pollinated).

B.—Bracteoles with rudimentary seeds. D.—Seed hops (artificially pollinated).

E.—Seedless hops (control—not pollinated).

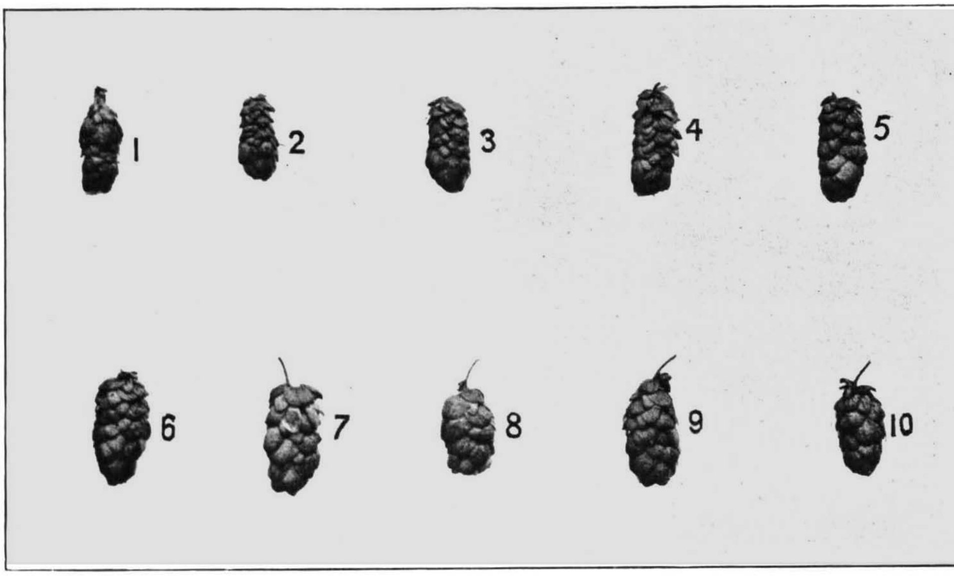


Fig. 4.—Partially Seedless and Seed Hops.

1.—Seedless in the middle only. 2–5.—Seedless at the stalk end only.

6–10.—Uniformly seeded and normally developed hops.

Fig. 5.—Hops attacked by Mould in the Seedless Portion.

1.—Attacked at the free end. 2.—Attacked at the stalk end.

3–5.—Fully developed fertile bracteoles in mouldy hops. 6–11.—Attacked in the seedless portion.