G. Mendel's Law Concerning the Behavior of Progeny of Varietal Hybrids

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The latest publication of Hugo de Vries: Sur la loi de disjonction des hybrides[1] which through the courtesy of the author reached me yesterday, prompts me to make the following statement:

In my hybridization experiments with varieties of maize and peas, I have come to the same results as de Vries, who experimented with varieties of many different kinds of plants, among them two varieties of maize. When I discovered the regularity of the phenomena, and the explanation thereof — to which I shall return presently — the same thing happened to me which now seems to be happening to de Vries: I thought that I had found *something new.*[2] *But then I convinced myself that the Abbot Gregor Mendel in Brünn, had, during the sixties, not only obtained the same result through extensive experiments with peas, which lasted for many years, as did de Vries and I, but had also given exactly the same explanation, as far as that was possible in 1866.*[3]

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1 Compt. rend. de l'Acad des Sciences, (Paris), 130, 1900, 26. mars.

2 See the postscript. (footnote added later).

3 Gregor Mendel, Versuche über Pflanzen-Hybriden. *Verh. des Naturf. Vereines in Brünn*, 4. 1866.

Today one has only to substitute "egg cell" or "egg nucleus" for "germinal cell" or "germinal vesicle" and perhaps "generative nucleus" for "pollen cell." An identical result was obtained by Mendel in several experiments with Phaseolus, and thus he suspected that the rules found might be applicable in many cases.

Mendel's paper, which although mentioned, is not properly appreciated in Focke's "Pflanzenmischlingen," and which otherwise had hardly been noticed, is among the best that has ever been written about hybrids, in spite of some objections which one might raise with respect to matters of secondary importance, e.g. terminology.

At the time I did not consider it necessary to establish my priority for this "re-discovery" by a preliminary note, but rather decided to continue the experiments further.

In the following I shall limit myself to an account of the experiments with varieties of peas.[4] Inter-varietal hybrids of maize show identical behavior in all essential points, but are more difficult to experiment with, and I have not yet elucidated to my satisfaction several points of secondary importance. They will be discussed somewhere else.

Varieties of peas are invaluable for the problem which interests us here, as Mendel had emphasized correctly, since the flowers are not only autogamous, but are very rarely fertilized by insects. On the basis of experiments on the formation of xenia — which, in the case of peas yielded only negative results — I came across this material. When I realized, that the rules here are much clearer than they are in maize, where I had first discovered them, I continued the observations.

The *characters* which differentiate the varieties of peas, can, as in all other cases, be grouped into *pairs*, each member having an effect on the same trait, one in one and the other in the other one of the varieties e.g. the color of the cotyledons, the color of the flower, the color of the seed coat, the hilum of the seed, etc. In many pairs one character, or rather the anlage thereof is so much stronger than the other character, or its anlage, that the former alone appears in the hybrid plant, while the latter does not show up at all. This one may be called the *dominant*, the other one the *recessive* anlage. Mendel named them in this way, and, by a strange coincidence, de Vries now does likewise. For example, the

4 The names of the varieties given in this paper are those which I received from Haage and Schmidt in Erfurt.

yellow color of the cotyledons is dominant over the green color, and red flower color over white flower color.

I can not understand why de Vries assumes that in all pairs of characters which differentiate two strains, one member must always be dominant.[5] Even in peas, where some characters completely conform to this rule, other character pairs are also known, in which neither character is dominant, as for instance the color of the seed coat, being either reddish-orange or greenish-hyaline.[6] In this case the hybrid may show all transitions, (this is true especially for the seed coat of peas), or it shows either more of one or of the other character (for example in hybrids of stocks; here a certain hybrid may be *just barely* distinguished from one parental form by its hardly noticeable slighter covering of hairs, although with some care, separation is always possible, while it is *highly distinct* from the other, i.e., the glabrous parental type).

The following holds only for pairs of characters which have a dominant and a recessive member; there is no reason to believe that it may not hold for other types of pairs of characters as well, but at present we know of no example.[7] Let us first consider a single pair of characters. It is immaterial whether the varieties to be crossed are only differentiated by this one pair, or by others as well. The specific pair of characters we may select is the *color of the embryo, either yellow or green.* It is very easy to obtain large numbers for this trait.

The facts, which Mendel found, I can fully confirm. They also agree with the findings of de Vries for his experimental objects. They are as follows:

1. In the first generation, all hybrid individuals are uniform and only the dominant character appears. In our special case the cotyledons are yellow.
2. When these seeds with yellow embryos are sown, plants are obtained, whose pods, which were produced by self-

5 For instance "D'autre part, l'étude des caractères simples des hybrides peut fournir la preuve la plus directe du principe énonce. *L'hybride montre toujours le caractère d'un des deux parents, et cela dans toute sa force;* jamais le caractère d'un parent, manquant a l'autre, ne se trouve réduit de moitié." (l.c. paragraph 3, italics mine).

6 The color of the hilum on the other hand (whether black, brownish etc. represents a dominant character.

7 In the meantime I have found an example (Footnote added later).

fertilization, contain seeds with *yellow* embryos and seeds with *green* embryos, (the second generation) and on the average, there are *three* yellow ones for each green *one.* If there are four or more seeds in each pod, one containing a green embryo will usually be among them.

3. When the seeds with a *green* embryo are sown, plants are obtained, whose pods, which were produced by self-fertilization, contain *only* seeds with *green* embryos, (the *third* generation). These, in turn, produce only seeds with *green* embryos, (the *fourth* generation), etc. With respect to this character, the *recessive* one, they behave like the *pure* variety, which carries it.

4. If the seeds with *yellow* embryo are sown, plants are produced which may be grouped into two *classes,*

   Class A, those plants, whose pods, which were obtained by self-fertilization, contain only seeds with yellow embryos (the *third* generation) and

   Class B, these plants, whose pods, which were produced by self-fertilization, contain seeds with *yellow* as well as seeds with *green* embryos (the *third* generation). Numerically, there are again on the average *three* seeds with *yellow* embryos for each *one* with a *green* embryo, just as in the second generation (see paragraph 2).

   The *number of individuals* in classes A and B is approximately *one* to *two.*

   Let me emphasize again, that embryos of Class A do not differ in their appearance in any way from those in Class B, only after the pods, which were produced by self-fertilization, have been harvested, can it be decided to which one of the classes the seed belonged.

5. Seeds with yellow embryos, which descended from plants of Class A (paragraph 4), produce plants, whose pods, which originated by self-fertilization, again contain only seeds with yellow embryos (the fourth generation). Plants which develop from them in turn produce only seeds with yellow embryos etc. As regards this character, the dominant one, they behave like the pure variety which carries it.

6. The seeds with green embryos, which are obtained from plants of Class B (paragraph 4, B) produce plants, whose pods, which originated by self-fertilization again contain only seeds with green embryos (the fourth generation). Plants which

develop from them in turn produce only seeds with green embryos, (the fifth generation) etc.; — just as did the green embryos of the second generation (paragraph 3).

7. The seeds with *yellow* embryos, which are obtained from plants of *Class B* (paragraph 4, B) again produce, just as it was described in paragraph 4, *two types of plants,* in the ratio *one* to *two,* whose seeds behave in the same way as described in paragraphs 5 and 6 and so forth.

The following table explains and summarizes the results discussed above, it also gives the numerical ratios.

TABLE 1

Parents	Hybrid					
	I. Gen.	II. Gen.	III. Gen.	IV. Gen.	V. Gen.	VI. Gen.
green		1 green..	∞ green..	∞ green..	∞ green..	∞ green
			1 green..	∞ green..	∞ green..	∞ green
				1 green..	∞ green..	∞ green
					1 green..	∞ green
						1 green
					2 yellow	
	∞ yellow	2 yellow	2 yellow	2 yellow	3	3 yellow
				3		
					1 yellow..	∞ yellow
			3			
				1 yellow..	∞ yellow..	∞ yellow
		3				
			1 yellow..	∞ yellow..	∞ yellow..	∞ yellow
yellow		1 yellow..	∞ yellow..	∞ yellow..	∞ yellow..	∞ yellow

The sign ∞ indicates that all of the seeds of the progeny in this group contained like embryos.

The two following tables show the results obtained in two of my experimental series. The generations are given in vertical sequence. The upper *figure in boldface* denotes in each generation the *number of embryos obtained*, the *figure in light face* the *number of individuals,* which were raised from these embryos and produced fruits; ye – yellow, gr – green. The rest is self-explanatory.

EXPERIMENT I

Hybrid between the "green late [variety] Erfurter Folgererbse" with green embryos and the "[variety] Kneifelerbse with purple-violet pods," having yellow embryos.[8]

EXPERIMENT II

Hybrid between the "green, late [variety] Erfurter Folgererbse," with green embryos and the [variety] "Bohnenerbse," with yellow embryos.

The numerical ratios of yellow embryos to green embryos are quite variable in individual plants. In experiment I the smallest percentages for green being 14.9 and 7.7 and the largest ones 44.2 and 10.0. — It is of no importance whether the dominant character was introduced by the paternal or by the maternal plant; in *all* varieties, which possess a specific pair of characteristics the latter behaves in the same manner.

TABLE 2

I Gener.				51 ye.		
				19		
II Gener.			619 ye.			206 gr. (25%)
			25			
	7 (28%)			18		11
III Gener.	251 ye.		550 ye.		195 gr. (26.2%)	538 gr.
			18			
	7	8 (44%)		10	14	10
IV. Gener.	224 ye.	216 ye.	225 ye.	70 gr. (23.8%)	370 gr.	307 gr.

8 Under identical conditions the plants produced an average of 43.3, 47.7, and 28.8 seeds in successive generations; this is a good example to show the consequences of self-fertilization, and also furnishes an explanation of the "giant growth' of some hybrids (footnote added later).

Experiment II. shows by chance the exact numerical ratios between the two classes of individuals which are produced by seeds with yellow embryos (7:14 = 1:2), while this ratio can be determined only from the mean of generations III and IV in experiment I: 15 [= 7(III) + 8(IV)] individuals in one class as opposed to 28 [= 18(III) + 10(IV)] of the other (34.9:65.1 instead of 33.3:66.6).

TABLE 3

I Gener.					31ye. 12	
II Gener.	7 (33%)		775 ye. 21 14			247 gr. (24.2%) 20
III Gener.	292 ye.	462 yr.		149 gr. (23.6%)		670 gr.

In order to *explain* the facts, one must assume (as did Mendel) that following fusion of the reproductive nuclei,[9] the anlage for one character, the recessive one, *(green* in our case) is suppressed by the other character, the dominant one, therefore all embryos are *yellow.* The anlage, however, although "latent" is preserved, and prior to *the definitive formation of the reproductive nuclei a complete separation of the two anlagen occurs, so that one half of the reproductive nuclei receive the anlage for the recessive character, i.e., green, the other half the anlage for the dominant character, i.e., yellow.* The earliest time at which this separation might occur is the time of formation of the primordial anlage of both the seed and the anthers.[10] The numerical ratio 1:1 strongly suggests that the separation occurs during a *nuclear*

9 Mendel, of course, does not mention nuclei, but only "germinal cells" and "pollen cells."

10 and at the latest at the time of the first division of the pollen grain nucleus from which the primary nucleus of the embryo sac is formed. For, in maize, it is shown by the similarity between the hybrid endosperm and the hybrid embryo that the two generative pollen tube nuclei and all of the eight nuclei of the embryo sac contain only one of the two anlagen. (Footnote added later).

division, the reduction division of Weismann[11] but, because of the numerous problems involved, a more detailed discussion would lead too far.

Thus among ovules, 500 contain the anlage for the dominant character (yellow), 500 the anlage for the recessive character (green), and among 1000 generative pollen tube nuclei there are also 500 each with the dominant (yellow) and with the recessive character (green). If the reproductive nuclei are brought together by chance, then the probability that among 1000 nuclear fusions two anlagen *of the same kind* will meet (either two dominant or two recessive ones) is equal to the probability of *two different* anlagen meeting (one dominant, one recessive). Thus each type of combination will occur 500 times, or in 50 percent of all of the combinations.

In the first case, i.e. when *like* anlagen meet, the probability that they will be two *recessive* ones is as great as that they will be two *dominant* ones, again one half, or each one will occur 250 times or in 25 per cent of all combinations. For the pair of characters under investigation, the result is here the same, as if two reproductive nuclei of either one of the pure varieties would unite.

In the second case — when *different* anlagen are combined the result of self-fertilization must be the same as that found in hybrids of the first generation, which were produced by experiment. The dominant anlage suppresses the recessive one, but later, preceding definitive formation of the reproductive nuclei, the two anlagen separate again, as was described for the artificially produced hybrid. “There occurs, accordingly a repeated hybridization” (Mendel).

The progeny of the first generation must consequently be separable into three classes, 25 percent having *only* the recessive, 25 percent having only the dominant and 50 percent having *both* characters, although [in the latter] only the dominant character may be recognized. — It follows from this assumption that in the first two cases all future generations will breed true for one of the two characters, while in the third case segregation will occur again.

If the hybrid (in the first generation) is pollinated with pollen of that parental variety which has the *dominant* character, instead of with its *own* pollen, only plants which show the *dominant* character are obtained, but among their progeny *one half* will in turn produce *only* individuals with the *dominant* character, while *the other half* produces some plants with the *dominant* and others with the *recessive* character, in a ratio of 3:1. If, on the other hand, the hybrid (first generation) is fertilized with the pollen of the parental variety with the *recessive*

11 See also “Keimplasma” p. 392 ff.

character, then *one half* of the plants obtained will show the *recessive* character, while the *other half* shows the *dominant* character, and the progeny of the *latter* again show the *dominant* and the *recessive* characters in a ratio of 3:1.

This theoretically derived rule also holds in the hybrids of maize.

Since two classes of individuals i.e. those with the dominant anlage only and those with both the dominant and the recessive anlagen, cannot be distinguished from one another externally, the correct numerical ratios can only be determined by *self-fertilization.* Since self-fertilization normally occurs in peas, they are such excellent experimental objects.

A further consequence of the above is the following: as long as, because of chance selection, the number of individuals of a plot remains constant in successive generations, the number of individuals in the modal class, *i.e.,* those containing both anlagen, decreases steadily, until they finally disappear completely. In the second generation they make up 50 percent of the total, 25 percent in the third generation, 12.5 in the fourth, 6.25 in the fifth and $100/2^{n-1}$ percent in the nth generation. This numerical decrease of the modal class had already been derived by Mendel.[12]

Thus far we have considered only the behavior of those pairs of characters in which one member is dominant. The case of two or more differentiating characters also was discussed *theoretically* and tested *experimentally* by Mendel. It was shown that all possible combinations occur as frequently as they are expected on the basis of the laws of probability, assuming that their production is due to chance. "It is demonstrated at the same time, *that the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks.*" (Mendel)[13]

In the case of *two* pairs of characters, *nine* different classes of individuals may occur. However, only *four groups* may be distinguished *externally*, the numbers of individuals in the classes must

12 One hardly needs to point out, how important this behavior is in regard to the question of species formation from hybrids. (Footnote added later).

13 There are again exceptions to this rule; strains with linked characters exist. (Footnote added later).

occur in a ratio of 9:3:3:1. Among 1000 individuals, 562.5, 187.5, 187.5 and 62.5 respectively will be grouped together. In a suitable experiment Mendel did obtain the numbers 315, 101, 108, and 32 respectively, which on the basis of 1000 are as 566.6, 181.6, 194.4 and 57.6. This is a good approximation to the ratio. With hybrids of maize I have obtained the same result, in one case, for instance, the numbers 308, 104, 96, and 37 or, calculated on the basis of 1000, 565, 191, 176, and 68.

Mendel concludes *“that the pea hybrids form egg and pollen cells which, in their constitution, represent in equal numbers all constant*[14] *forms which result from the combination of the characters when united in fertilization.”* We may say in the terms used in this paper: *In the hybrid reproductive cells are produced in which the anlagen for the individual parental characteristics are contained in all possible combinations, but both anlagen for the same pair of characters are never combined. Each combination occurs with approximately the same frequency*. — If the parental strains differ only in *one* pair of characters (2 characters: *A, a)* the hybrid will form only *two types* of reproductive nuclei (*A, a)* which are like those of the parents. Each type is 50 percent of the total. If the parents differ in *two* pairs of characters (4 characters: *A, a; B, b) four types* of reproductive nuclei will be formed, *(AB, Ab, aB, ab)* and 25 percent of the total will be of each type. If the parents differ in *three* pairs of characters (6 characters: *A, a; B, b; C, c) eight types* of reproductive nuclei will be formed *(ABC, ABc, AbC, Abc, aBC, aBc, abC, abc),* and 12.5 percent of the total are of each type.[15]

This I call Mendel’s law. It includes the “loi de disjonction” of de Vries, also. Everything else may be derived from this law.

At present, however, this law is applicable only to a certain number of cases, i.e. those where one member of a pair of characters is dominant,[16] and probably only to hybrids between varieties. It seems impossible that all pairs of characters of all hybrids should behave according to this law. Some hybrids of peas bear this out.

In the *first* generation of the combination of the “green, late [variety] Erfurter Folgererbse” with an almost colorless seed coat, and the “[variety] Kneifelerbse with purple-violet pods,” or the “[variety]

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14 Mendel calls a type constant, if it no longer contains the two different anlagen of a pair of characters.

15 If the pollen grains of the two parental strains differ externally, one may, if Mendel’s law holds, expect the hybrid to form two externally different types of pollen grains. That this is true was first observed by Focke.

16 See footnote 6 p. 6.

Pahlerbse with purple pods" both having a solid-color, orange-red seed coat, which turns brown on aging, the seed coats within the same pod were sometimes colorless, sometimes intensely red, *but usually more or less tinted with orange*, and also speckled to a variable degree with purplish-black spots. Thus, in addition to a *dilution* of one of the characters, an (apparently) *new* character had originated. In the second generation, however, the seeds which show the two extremes of coloration, i.e. those with orange red, and those with almost colorless seed coats will again produce the extreme types and all of the transitions between them. The speckling was sometimes unchanged, sometimes not present at all or very slight and sometimes somewhat increased. Size and shape of the seed and texture of the seed surface behaved in a similar way.

I will discuss these points at a later time.

Tübingen, 22 April 1900

POSTSCRIPT (ADDED IN PROOF)

In the meantime de Vries has published in these proceedings (No. 3 of this year) some more details concerning his experiments. There he refers to Mendel's investigations, which *were not even mentioned in the "Comptes rendus."* I must emphasize again:

1. *that in many pairs of characters there is no dominant member* (p. 41),
2. *that Mendel's law of segregation cannot be applied universally*. (p. 47).

Tübingen, 16 May 1900