Citation:

Tammes, T., Some correlationphenomena in hybrids, in:
KNAW, Proceedings, 15 II, 1912-1913, Amsterdam, 1913, pp. 1004-1014

Botany. — *"Some correlationphenomena in hybrids"*. By Miss T. Tammes. (Communicated by Prof. Moll).

(Communicated in the meeting of November 30, 1912).

In recent years there have been observed also in hybridisation phenomena which show a certain relation between different characters of a plant. Already in 1900 Correns[1]) pointed out this relation and called it "Faktorenkoppelung". Some years later Bateson[2]) put forward a theory to explain the phenomena observed. According to Bateson, in the formation of gametes in the case of a plant heterozygous for more than one factor, the various possible combinations of factors or genes do not arise in equal numbers. There may be two reasons for this. In the first place some factors may show a certain tendency to remain connected whilst they are however not so completely coupled as to preclude occasional separation. In the second place there can be between different factors a tendency to repulsion.

Some examples of such "gametic-coupling" and "repulsion" or "spurious allelomorphism", as Bateson calls these phenomena, are already known. I too made observations in the course of my investigation on hybridisation that could best be explained by such a genetic correlation. Whilst however the cases known up to the present relate to characters whose presence or absence in the plants investigated is easily determined, this is not so in my inquiry. I have studied characters whose fluctuating variability is very marked. while moreover the distinction between the parental forms for one and the same character already amounts to several genes. The characters are, as Lang[3]) expresses it, polymeric. On this account the phenomena become so complicated that a complete analysis is impossible or only possible by most laborious investigation. I have so far therefore taken a shorter course and shall only show in this preliminary paper that the phenomena point to a correlation not only between two but indeed between a greater number of characters.

My observations have been made on the cross already[4]) earlier described, between *Linum angustifolium* Huds. and a variety from

[1]) C. Correns, Ueber *Levkoyen*bastarde. Bot Centr. Bd. 84, 1900, p. 11 of the reprint.

[2]) W. Bateson, Mendel's Principles of Heredity. 1909, p. 148.

[3]) Arnold Lang, Fortgesetzte Vererbungsstudien. Zeitschr. f. indukt. Abst. und Vererbungslehre, Bd. V, 1911, p. 113.

[4]) Das Verhalten fluktuierend variierender Merkmale bei der Bastardierung. Rec. d. Trav. bot. Néerl. Vol. 8, 1911. p. 201.

Egypt of *Linum usitatissimum* L. which I have called *Egyptian flax*. The chief points of difference between these plants are the following: the flower, the fruit and the seed of *L angustifolium* are smaller than those of *Egyptian flax,* and moreover the colour of the flower is lighter.

The following mean values show this.

	L. angustifolium.	*Egyptian flax.*
Length of petal	8.08 mm	16.20 mm
Breadth ,,	4.45 ,,	13.05 ,,
Length of seed	2.40 ,,	6.08 ,,
Breadth ,,	1.54 ,,	2.94 ,,

By analysis of the second generation I was able to show that the difference in length of the petal of the two forms is caused by at least four factors. This holds good also for the breadth of the petal, while the difference for the length of the seed amounts to at least four and for the colour of the flower to at least three factors. The difference in breadth of the seed is also caused by several factors. [1])

I have attempted to trace the behaviour of the above characters on hybridisation. The first generation was uniform and intermediate in the case of all characters; in the second generation a considerable segretation had occurred. This generation consisted for each of the reciprocal crosses of fully 100 plants. Both groups were separately investigated. Since these however gave exactly the same results, I will only deal with the crossing in which *L. angustifolium* was the father. Of this I have observations of all characters in exactly 100 plants.

The length and breadth of the petal were determined by taking the average values of several flowers; for the determination of the length and breadth of the seed a greater number of seeds were measured, mostly 50 to 100, and the average was taken. The colour of the flower was estimated in the manner described before [2]) and expressed numerically. The light colour of the flower of *L. angus-*

[1]) Since the appearance of my above mentioned paper I have succeeded in showing that the factors which cause the difference in the colour of the flower are distributed over both forms and that these forms have no common factors The proof of this was obtained by the appearance of white flowers. The plant was found in much larger culture than the one previously grown. In this case the hybrid thus oversteps the limits of the characters in the parents.

With respect to the factors for the other characters my investigations are not yet complete.

[2]) l. c. p. 260.

Length of seed in mm	Breadth of seed in mm	Length of petal in mm	Breadth of petal in mm	Colour of petal
3.144	1.880	9.7	6.3	3
3.186	1.961	10.8	8.0	5
3.186	2.006	10.0	8.3	4
3.224	1.920	9.4	7.0	1
3.242	1.976	9.5	6.4	2
3.281	2.007	10.6	8.0	3
3.305	1 960	9.4	8.5	6
3.321	1.895	10.5	7.8	5
3.383	2.054	11.4	9.4	6
3.387	1.916	10.1	7.5	5
3.405	1.983	9.5	7.7	5
3.449	1.960	10.0	8.0	2
3.450	2.006	11.0	7.0	6
3.451	2.016	10.9	8.3	6
3.458	2.095	9.6	7.0	4
3.473	2.057	11.1	9.2	8
3.482	2.023	11.0	8.3	7
3.495	1.928	11.0	8.5	7
3.501	2.104	10.8	8.9	8
3.511	2.038	10.0	8.0	6
3.529	2.022	11.5	8 0	6
3.530	2.042	9.2	7.3	4
3.552	2.067	10.6	8.0	4
3 557	2.086	11.3	7.5	5
3.562	2.239	10.5	7.0	6
85.064	50.241	259.4	195.9	124

Length of seed in mm	Breadth of seed in mm	Length of petal in mm	Breadth of petal in mm	Colour of petal
3.564	2.130	10.8	8.8	7
3.570	1.993	10.3	8.5	7
3.575	2.149	10.8	7.5	5
3.600	2.126	10.8	8.4	8
3.606	2.077	9.4	6.9	5
3.610	2.224	11.8	8.6	7
3.615	2.088	10.8	8.8	6
3.617	2.080	10.4	8.0	5
3.619	2.150	10.8	7.5	6
3.620	2.112	10.5	7.8	5
3.624	2.137	10.7	8.6	7
3.628	2.246	11.5	9.0	7
3.629	2.333	11.2	7.4	4
3.629	2.157	10.6	8.4	8
3.648	2.013	10.7	8.9	2
3.650	2.145	10.5	8.4	3
3.662	2.226	12.1	8.6	3
3.670	2.081	10.6	7.8	6
3.671	2.050	11.2	7.0	5
3.672	2.036	10.0	6.3	5
3.682	2.193	10.7	6.9	9
3.716	2.267	11.4	8.2	6
3.717	2.331	12.4	9.2	8
3.723	2.183	10.3	7.5	6
3.741	2.141	11.2	8.0	5
91.058	53.668	271.5	201.0	145

Length of seed in mm	Breadth of seed in mm	Length of petal in mm	Breadth of petal in mm	Colour of petal
3.759	2.200	10.8	7.0	4
3.761	2.075	11.0	8.2	5
3.766	2.027	11.5	7.6	5
3.767	2.067	11.2	8.4	6
3.771	2.209	10.4	8.0	9
3.773	2.075	10.0	7.5	4
3.781	2.250	11.2	8.5	6
3.786	2.198	10.1	8.7	10
3.791	2.181	10.2	8.2	7
3.798	2.227	11.0	9.5	7
3.803	2.147	11.8	9.6	6
3.821	2.149	11.3	8.0	8
3.829	2.213	13.0	8.6	4
3.829	2.228	10.0	7.4	7
3.830	2.170	11.0	9.2	8
3 830	2.224	11.2	9.5	6
3 831	2.268	10.5	7.8	7
3.835	2.135	11.5	8.5	5
3.841	2.204	9.5	6.5	5
3.843	2.171	10.6	8.0	4
3.861	2.249	11.7	8.5	5
3.890	2.180	9.8	7.0	6
3.906	2.320	11.5	8.2	8
3.908	2.175	11.3	8.5	4
3.910	2.202	10.0	8.6	4
95.520	54.544	272.1	205.5	150

1009

Length of seed in mm	Breadth of seed in mm	Length of petal in mm	Breadth of petal in mm	Colour of petal
3.915	2.260	10.7	9.0	8
3.922	2.413	10.0	8.4	4
3.922	2.313	11.0	8.5	8
3.923	2.270	10.0	9.1	5
3.926	2 287	10.6	8.2	9
3.933	2.271	11.0	9.5	8
3.940	2.351	11.7	9.8	8
3.948	2.361	12.0	9.2	7
3.949	2.150	11.0	8.8	9
3.968	2.298	10.5	8.0	6
3.988	2.196	10.6	9.5	8
4.016	2.218	9.5	8.2	4
4.031	2.225	11.5	8.2	8
4.139	2.295	11.3	9.7	6
4.140	2.317	11.0	8.0	5
4.154	2.350	12.0	9.5	7
4.167	2.389	11.3	8.0	6
4.188	2.345	11.3	8.6	7
4.238	2.348	11.2	9.3	9
4.244	2.456	11.0	9.4	5
4.274	2.446	11.8	9.8	10
4.335	2.452	13.2	10.7	8
4.350	2.311	11.2	7.5	6
4.381	2.461	12.2	10.0	7
4.420	2.469	11.5	9.9	7
102.411	58.252	279.1	224.8	175

tifolium was represented by 1, the much darker colour of *Egyptian flax* by 10.

I have arranged the observations according to the ascending values of the length of the seed in order to obtain a survey of the mutual relationship of the various characters.

In the preceding table the figures placed in a horizontal row refer to the various characters of the same plant, in the vertical columns those for different plants are given. The whole table is divided into four parts, each containing 25 plants.

From these tables it must now be clear whether there is or is not an inter-relation between the length of the seed and the other characters. If the latter are wholly independent of the former then for each character the values in a vertical direction must follow each other without any regularity; the lowest average, and highest values for each character must be distributed equally over the four tables and the totals of the 4 successive series must be equal or nearly equal or must at least be arranged without any regularity.

On the other hand should there exist an intimate relation between the length of the seed and the other characters such that they behave as a single whole, then these other characters will also be arranged in the tables according to ascending or descending values, except for small deviations due to the influence of external circumstances.

A superficial inspection already shows that for none of the characters are the values in the vertical columns in a sequence; between successive figures a good many irregularities occur. If however the tables are compared with one another, it is seen that in general in the first lower values, in the last higher values are found.

In order to make a comparison easier, I have added the values for the 25 plants of each table. Below are given the totals obtained for the different characters.

Length of seed	Breadth of seed	Length of petal	Breadth of petal	Colour of petal
85.064	50.241	259.4	195.9	124
91.058	53.668	271.5	201.0	145
95.520	54.544	272.1	205.5	150
102.411	58.252	279.1	224.8	175

We see the values for all four characters increase in successive series. It follows therefore that, on the whole, in the plants which have the smallest length of seed, the breadth of the seed and the length and breadth of the petal are small, whilst moreover the flower shows the lighter shades, and conversely a greater length of seed is generally coupled with greater breadth and a larger, more deeply-coloured flower.

In the same way as proceeding from the length of the seed, I have also determined the inter-relations of the other characters. From the above table I have arranged the values in ascending order according to the breadth of the seed and compared the others with it. The same was done starting from the other characters. It is unnecessary to give here the complete tables. Below are set out the totals obtained each time for 25 successive plants.

Arranged in ascending order of breadth of seed	Length of petal	Breadth of petal	Colour of petal
Plant 1— 25	261.3	195.8	121
„ 26— 50	269.0	204.5	148
„ 51— 75	270.0	205.0	154
„ 76—100	282.8	221.9	171

Arranged in ascending order of length of petal	Breadth of petal	Colour of petal
Plant 1— 25	190.8	121
„ 26— 50	201.3	148
„ 51— 75	211.7	160
„ 76—100	223.4	165

Arranged in ascending order of breadth of petal	Colour of petal
plant 1— 25	124
„ 26— 50	141
„ 51— 75	150
„ 76—100	178

As is seen the values for successive series of 25 plants in all the above cases increase. There exists therefore a relation not only between the length of the seed and the other characters but the five characters together form a complex of which each part in its development depends somewhat upon all the rest.

Now the nature of the inter-relation of the characters of the flower and seed which have been studied is, as the figures show, such that in general the development of all characters in one plant is in the same direction, since, for example, a long petal shows a distinct tendency to be coupled with a broad petal, with darker shade of flower and with a greater length and breadth of the seed.

From this it might be deduced that here it is only a question of ordinary consequences of slight differences in external conditions in consequence of which the best nourished plants develop more strongly and form larger deeper-coloured flowers and larger seeds, in other words that the relation observed may only be the usual correlation phenomenon of fluctuating varying characters, just as met with in homogeneous material that is in pure forms.

There indeed occurs, as the observations showed, a correlation between the characters in the parent forms and also in the first generation, of the same kind as the relation here described.

In F_2 also this correlation will play a more certain part, but only in a subsidiary way and the phenomenon is chiefly due to another cause. This is already clear from my earlier investigations. Moreover I have also traced the relationships in the offspring. When the relation observed is a phenomenon of correlative variability, then the offspring of each individual of the second generation must exhibit again the same correlationfigure as the whole second generation or at least the offspring of a plant which is extreme for one or more characters must in general deviate much less from the average type than this plant itself. Now this was not the case, for it was found that the relationships as they appeared in the F_2-plant were in the main handed on to the offspring. Some examples having reference to the length, breadth, and colour of the petal will make this clear. The values for four different F_2-plants and their offspring are given in the following table. The first F_2-plant possesses the three characters in an extreme degree, the fourth has extremely small values for them all, the two others show different combination.

	F_2	F_3
Length of petal	13.2 mm	12.1—14.8 mm
Breadth ,,	10.7 ,,	10.3—12.2 ,,
Colour ,,	8	7—9
Length of petal	13.0 mm	12.1—14.0 mm
Breadth ,,	8.6 ,,	7.7—9.2 ,,
Colour ,,	3	2—5

	F_2	F_3
Length of petal	10.0 mm	8.5—11.2 mm
Breadth ,,	9.1 ,,	8.3—10.1 ,,
Colour ,,	5	3—7
Length of petal	9.5 mm	8.2—10.0 mm
Breadth ,,	6.4 ,,	6.0— 7.2 ,,
Colour ,,	2	1—2

The above proves that there is still another relation between the characters in the plants studied in addition to ordinary correlation. The whole phenomenon is only superficially like such a correlation.

Just as any single character which is based on several genes, gives in the second generation a pseudo-curve which shows itself as a curve of fluctuating variability but in which the fluctuating variability plays only a more or less subordinate role, so also here in F_2 an inter-relation of different characters may appear that simulates ordinary correlation, but that is in reality a completely different phenomenon which is only slightly affected by this correlation. I point this out because it seems to me that in studying correlative variability it is of the highest importance to investigate only pure homogeneous material. Since JOHANNSEN has made known to us the "pure lines", it has become clear that much that was formerly thought to be pure material, is a mixture of several forms perhaps also of hybrids. It is possible that the correlation found in such material is not a pure correlation between the fluctuating variability of the characters but is wholly or in part a different correlation phenomenon. This is also the case here. We must assume that here a genetic relation exists between the groups of factors for the different characters. This relation is such that in the formation of gametes in F_2 definite combinations of factors occur preferentially. In general a tendency exists to make the proportion in the number of factors for the various characters such as it was in the original forms or at least to approximate to these. This explains that in F_2 more forms arise in which the characters all deviate in the same direction from the average than should be the case according to the laws of probability.

In the crossing mentioned above the groups of factors for the various characters behave with respect to one another differently from the way in which the factors for one single character behave mutually; for my earlier investigations have shown, that for each of the characters under discussion the genes are mutually quite independent of one another. It is most noteworthy that there exists between the factorgroups for different characters a closer relation than between the factors for the same. Further investigations must show to what extent this phenomenon occurs in other cases and whether it is always coupled with a tendency to preserve the complete image of the parent forms.

In the case here described the genetic correlation is incomplete. As is clear from the tables plants are found, which for some characters more nearly approach the one parental form and for others are nearer to the second. The number in which the different combinations occur, cannot be determined as is done by other investigators for their crossings, also because ordinary correlation plays through it and still further obliterates the separation between the groups. If at all, the ratios could only be found by much more detailed investigation; but it is clear from the foregoing that by this means some insight into the phenomena may be obtained.

The characters mentioned all belong to flower or seed, the fruit might be added since a very close relation exists between the size of the fruit and that of the seed. I am also engaged in tracing the relation of the characters mentioned to those of the vegetative organs. I am, however, prevented by circumstances from completing this investigation in the near future.

The results of the investigation may be summarised as follows: In hybrids of *Linum usitatissimum* and *L. angustifolium* an incomplete genetic correlation exists between the groups of factors or genes for length, breadth, and colour of the petal and length and breadth of the seed; whereas on the other hand the factors for the same character are completely independent of one another.

The inter-relation is such that there exists a tendency to approximate to the combination of characters as it occurs in the parent forms.

The genetic correlation expresses itself apparently as a phenomenon of the ordinary correlation of fluctuatingly varying characters; the latter correlation which also occurs, plays only through the former.

Botanical Laboratory.

Groningen, 3 Oct. 1912.