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The difficulties may be removed if $e^{\frac{\psi-E}{\vartheta}}$ is considered as a value with dimensions 0, and then multiplied by a constant C to bring the dimensions into order.

The procedure is the same in other parts of Physics where exponential functions are used. Hence the relative density would now become $Ce^{\frac{\psi-E}{\vartheta}}$, or rather, because in this way we should get too many constants: $Ce^{-\frac{E}{\vartheta}}$, so that $\int Ce^{-\frac{E}{\vartheta}}=1$. Now we should have to take for the entropy not the mean $-\log P$ or $-\log C+\frac{E}{\vartheta}$, but the mean $-\log(P\times$ certain constant extension). If we now take g^N for this constant extension, so that the form within parentheses represents the relative number of systempoints over an extension element g^N, we get, after multiplication by the usual constant k, PLANCK's above discussed formula.

If besides we multiply the form, the logarithm of which is taken, by $N!$, we arrive at TETRODE's formula.

Botany. — *"On the mutual effect of genotypic factors."* By Dr. TINE TAMMES. (Communicated by Prof. J. W. MOLL).

(Communicated in the meeting of November 27, 1915).

The varieties of *Linum usitatissimum* L., which I have used for my crossing experiments, show three types with regard to the breadth of the petals. In two of these, however, the length of the petal is the same.

The broadest and also the longest petal belongs to the so called Egyptian flax. I have previously [1]) reported on the variability-curve and the median value of both length and breadth. In the present investigation, however, the use of the mean value was to be preferred, because in some cases the measurements could not be very numerous. Since this paper only deals with the breadth, it will suffice to give the mean value of this dimension only. It is 13.4 millimetres.

The breadth of the petal was formerly taken and is still taken to be the greatest breadth. The colour of the flower of Egyptian flax is blue and has been repeatedly discussed before.

[1]) Das Verhalten fluktuierend variierender Merkmale bei der Bastardierung. Rec. d. Trav. bot. Néerl. Vol. VIII, 1911, p. 249.

The second type, as regards breadth of the petals, occurs in the ordinary blue flax, commonly cultivated in the Dutch province of Groningen, and in the flax with white flowers, grown in some districts of the neighbouring province of Friesland. These two agree in the length and also in the breadth of the petals. For plants grown under identical conditions, the average breadth of the petals from 30 flowers, taken from 30 different individuals, was 7.0 mm. for the common blue flax and 7.1 mm. for the common white. The small difference between these values may here be neglected.

The third type of petal-breadth occurs in another variety with white flowers. This was formerly described under the names *Vilmorin* white[1]) and crisped white[2]). The latter name was applied to this variety to distinguish it from the common white flax, which like the common blue and the Egyptian, has quite flat petals, whereas in the crisped white flax the apical margin of the petal is somewhat crispy and rolled upwards at the sides. The petals are further distinguished from those of the common blue and white flaxes, by being much narrower. Since the margin is only crisped at the top and the rest of the lamina is flat, the greatest breadth is easily determined. In 50 different plants the breadth of a single petal was measured: the mean was 3.3 mm., i.e. less than half that of the other white and of the common blue flax. The length of the petal, however, is about the same on all three varieties. Thus for 50 petals the average was 10.1 mm., as against an average length of 10.6 mm. for the common white, and 10.3 mm. for the common blue flax. The Egyptian flax has much longer petals, their average length being 16.2 mm.

As is evident from the average values for the petal-breadth viz. 13.4, 7.1, 7.0 and 3.3 mm., the above mentioned varieties differ considerably in this character; two of the four belong to the same type as regards breadth, i.e. that of 7 mm., but these two differ in colour. This paper deals with the behaviour of the petal-breadth and the correlation between breadth and colour in the various crosses between the four varieties. For details regarding the behaviour of the colour of the flowers I refer to the above quoted paper of 1915. Here it is enough to know that on crossing a white with a blue variety, blue and white individuals occur in F_2. The ratios of these do not concern us here. First the successive crosses with

[1]) The explanation of an apparent exception to MENDEL's law of segregation. Proc. Kon. Akad. v. Wetensch. Amsterdam Vol. XVI, 1914, p. 1021.

[2]) Die genotypische Zusammensetzung einiger Varietäten derselben Art und ihr genetischer Zusammenhang. Rec. d. Trav. bot. Néerl. Vol. XII, 1915, p. 219.

their attendant phenomena will be described, and then conclusions will be drawn from the observations.

The common blue and the common white flax, differing in colour but having the same average petal-breadth viz. 7 mm., when crossed, give only progeny of the same type of breadth. This shows that these two varieties have the same factor or factors for breadth of petal. Since the blue and the white offspring agree in breadth, there is evidently in this crossing no relation between breadth and colour of the petal.

The common blue flax (7 mm.) and the Egyptian flax (13.4 mm.) differ, in contradistinction to the varieties of the previous cross, in breadth, but not in colour. The phenomena, observed in this cross with regard to breadth, have been previously [1]) described by me in detail. The following excerpt from this paper will suffice. The first generation is intermediate, the breadth of the petal is about the average of that of the parents. In the second generation segregation into various types of breadth occurs. On account of fluctuating variability the limits between the different groups cannot, however, be observed and all transitional states between the breadth of the common flax and that of the Egyptian are found, but in definite ratios. The most frequent breadth in F_2 is approximately the mean of the P-varieties, and the number of individuals having any particular breadth diminishes, the nearer this breadth approaches that of the P-forms. All F_2-individuals together give a curve for the breadth, apparently corresponding to a variability-curve. The deduction from the whole set of observations was, that the Egyptian flax has, compared with the common blue, a few more ordinary Mendelian factors for broadness. Since the whole offspring is blue and nevertheless differs in breadth, the colour and breadth of the petals are evidently independent of each other in this crossing also.

In the cross between the common white flax (7 mm.) and the Egyptian (13.4 mm.) which differ in colour, as well as in breadth, the phenomena observed with regard to breadth are the same as those in the preceding cross. Here also the first generation is intermediate and in the second generation every transition between the breadth of the white and that of the Egyptian flax occurs in the ordinary manner. From this we may deduce, that these two varieties also differ in factors for broadness and that the Egyptian flax has a few more factors than the common white. The observations further show that, in this case also, there is no interdependence

[1]) l. c. Vol. VIII, 1911, p. 253.

between breadth and colour. For in the second generation there occur among the white, as well as among the blue flowers, narrow, broad and intermediate petals of every kind, although the white *P*-variety is narrower than the blue. The factors for broadness and for colour evidently follow MENDEL's law of segregation independently.

On the other hand the behaviour of the breadth and its relation to colour is quite different in the cross between the common blue (7 mm.) and the narrow-petalled white flax (3.3 mm.). These two varieties, like the preceding pair, differ in breadth as well as in colour. Here, however, all the blue descendants agree in breadth with the common blue flax and all the white ones with the narrow-petalled white. Although the two *P*-varieties, as in the two previous crosses, differ in breadth, there are here no transitions. Two sharply separated groups arise, one with broad blue petals and the other with narrower white ones, each agreeing with one of the two varieties crossed. In this case there is therefore a connection between breadth and colour, in contradistinction to the crosses previously discussed; the broader petals are always blue, the narrower ones always white.

Knowing only the phenomena occurring in this cross, one would doubtless feel convinced, that one and the same factor, or a group of completely coupled factors produces here simultaneously the superior breadth and the blue colour of the petal. We learn, however, from the investigation of another cross, namely between the Egyptian (13.4 mm.) and the narrow-petalled white flax (3.3 mm.) which also differ both in colour and in breadth, that the relation of breadth to colour is a different one, although these factors are not wholly independent either, as was apparently the case in the crossings discussed first.

In this cross between the Egyptian flax and the narrow-petalled white variety, the first generation has blue petals intermediate in breadth between those of the parents. In the second generation the relation of white and blue individuals as to the breadth differs from that in the crosses already discussed.

Of 300 different white-flowered F_2-plants the breadth of the petals of one flower was determined and also of 300 plants with blue flowers. Whereas the petal-breadth in the narrow *P*-variety varies from 2.1 to 4.2 mm. and in the Egyptian flax from 10.5 to 16.4 mm., the white F_2-plants gave for the breadth 2.1 to 10.4 mm. and the blue F_2-plants 5.7 to 16.2 mm.

The white F_2-plants in general have much narrower petals than the blue. Hence two groups are formed, one with narrow white and the other with broader blue flowers. These groups do not, however, correspond to the white and blue P-varieties, as is the case in the cross between the narrow-petalled white and the common blue flax. The white ones are in general broader than the narrow-petalled white flax and the blue ones are on the whole narrower than the Egyptian. In both transitional breadths occur between the two P-varieties. Nevertheless the phenomena do not agree with those observed in the cross between the common white and the Egyptian flax, for, although transitions do occur, the white and the blue F_2-individuals are not identical in breadth, as in this last named cross. The white ones have no very broad, and the blue ones no very narrow petals. In order to determine the extreme limit, which both groups can reach, some of the white F_2-plants with the broadest petals were cultivated further From the third generation so obtained a few of the broadest were again selected for further culture, and similarly from the fourth and the fifth generation. Although the nutritional conditions were always most favourable, the greatest breadth observed in the 786 plants from the second to the sixth generation was 11.4 mm. This was in the fourth generation. Among the offspring of this plant in the fifth and sixth generation even this breadth did not occur again; the maximum in F_6 was 10.5 mm. Evidently therefore the very broadest white ones barely surpass the minimum breadth of the Egyptian flax and do not even reach its mean breadth.

In the same way the narrowest blue ones were cultivated further for some years, the conditions being made less favourable. The extreme minimum was found to be 5.7 mm. Blue flowers with petals of the breadth of the narrow-petalled white flax did not occur at all among the 722 plants investigated up to the fifth generation.

In this crossing then two groups are indeed formed, one with narrow white and the other with broader blue flowers. This was also found to be the case on further cultivation of the heterozygotic F_2- and F_3-plants; the whites were always on the whole narrower than the blue ones formed at the same time.

The way in which the breadth behaves in this crossing, is at first sight not in accordance with MENDEL's segregation-law. The two forms crossed show a great difference in breadth and among the offspring intermediate forms are also found. Yet the second generation does not show the ordinary phenomenon of Mendelian segregation, as is observed with characters which vary in a fluctuating manner, where the limits between the different groups formed in F_2 are obscured. In such cases the F_2-individuals together give a curve for the breadth which extends from the minimum of the narrowest to the maximum of the broadest form, with the summit near the average of the two P-forms. Here, however, the whole of the second generation gives a curve for the breadth, which indeed extends from the minimum of the narrow white to the maximum of the Egyptian flax, but which shows two summits between these. Since one part of the curve towards the minimum with one of the summits is formed by the white, and the other part with the other summit by the blue F_2-individuals, it is evident that there is here an interdependence between breadth and colour. Yet this relation is not simply, that blue colour is associated with broadness, because the same factor or factors simultaneously cause broadness and blue colour, or because the factors for broadness and those for colour are completely coupled, as is apparently the case in the crossing of the ordinary blue flax with the narrow-petalled white. If this were the case, then all the white offspring would have to show the type of broadness of the narrow-petalled white flax, and all the blue descendants the broadness-type of the Egyptian flax.

This is not so, however, for white petals occur, which are broader than the white P-variety and blue ones, narrower than the blue P-variety. In an attempted explanation we might assume *incomplete* coupling of the factors for broadness and for colour, leading to very complicated relationships. This is, however, a great disadvantage and we are induced to search for another explanation of this peculiar interdependence between the two characters, which here presents itself. Now previous experiments on the crossing of these varieties of flax have demonstrated [1]) the presence of various factors and it is a knowledge of these and of their action that enables us to give a satisfactory explanation, not only of the phenomena attending the last mentioned crossing, but also of the fact, that in the various crossings the behaviour of the breadth and the connection between breadth and colour are so varied.

Previously it was shown, that the genotypic composition of the common blue and of the Egyptian flax for the colour of the flower is represented, in the common blue and in the Egyptian flax, by the formula $AABBCC$, in the common white by $AABB$ and in the narrow-petalled white by $AACC$. The factors B and C acting conjointly, cause the blue colour, but are separately unable to produce a blue colour. Furthermore B and C exercise an influence on other characters, as was previously discussed in detail. A is an intensification-factor for the colour, but remains out of account here.

[1]) l. c. vol. XII, 1915, p. 217.

A crossing of two of the varieties which has not yet been discussed here, viz. of the common white with the narrow-petalled white, shows on the basis of their genotypic composition, that the narrow-petalled white flax, although it has much narrower petals than the common white, nevertheless possesses the same factors for the breadth.

For in this crossing there arise in F_2 white flowering individuals of the composition *AAbbcc*, in which therefore *B* as well as *C* are absent and which have the same breadth as the common white flax. This proves, that the factors *B* and *C* do not regulate the breadth of the petals, but that there are present other factors for breadth in the two varieties crossed. If these factors for breadth were different for the two varieties, then the above mentioned individuals would necessarily belong to different types of breadth, some narrow like the narrow-petalled flax, others broader like the common white or intermediate, possibly even narrower or broader than the *P*-varieties. This is not the case. All individuals of the composition *AAbbcc* are of the same type of breadth. From this it follows that the common white and the narrow-petalled white flax have the same factors for breadth. Nevertheless the narrow-petalled flax is narrower than the common white. There is therefore present in these varieties some cause which partially inhibits the factors for breadth. This must be the factor *C*, for as soon as this factor is wanting as in the above mentioned individuals in F_2 of the composition *AAbbcc*; the breadth is equal to that of the common white flax. This factor *C*, which together with *B*, gives the blue colour, is therefore seen to be an inhibiting factor for the factors of breadth. The factor *C* also occurs, however, in the common blue flax *AABBCC*, which is nevertheless not narrower than the common white flax. The reason for this must be the presence of factor *B* which prevents the inhibiting action of *C* on the factors for breadth. This agrees with what I have already published [1]) concerning the action of the factors *B* and *C* with reference to the crisping of the petal margin, the numbers of seeds per fruit and the germinating-power of the seed. For the factor *C* is also the cause of the crisping of the petal apex, of the diminution of the number of seeds per fruit and of the diminution of the germinating-power of the seed, whilst the factor *B* prevents this action of *C*. Here the same relation for broadness presents itself; *C* causes a diminution of breadth and *B* again abolishes the inhibiting action of *C*.

It is now necessary to examine whether indeed all the phenomena

[1]) l c. Vol. XII, 1915, p. 217.

observed in the different crossings are fully and satisfactorily explained by this conception of the occurrence of factors of breadth and the action of the factors B and C.

Common blue flax $AABBCC$ and common white $AABB$, which have the same breadth and when crossed give only offspring of this breadth, do not form in crossing a single individual in which the factor C occurs alone, i.e. without B. Either C is absent from the offspring as in the white, or B occurs together with C, as in the blue. The factors for broadness are not inhibited in any single individual and this explains why the white, as well as the blue offspring have all the same breadth.

In crossing the common blue flax $AABBCC$ with the Egyptian $AABBCC$, and the common white $AABB$ with the Egyptian $AABBCC$ there is not either produced any offspring in which C appears without B also. The factors for broadness were not inhibited in a single individual. The differences in breadth between the P-varieties of these two crossings will therefore not disturb the phenomena, which will present themselves in accordance with the law of segregation and this is indeed observed.

In the second crossing, namely that between the common white and the Egyptian flax, there exists in the P-varieties a difference in colour as well as in breadth, and it was observed that these two characters behave quite independently of each other. This now becomes clear, for C is absent from the white offspring and the action of C is inhibited by B in the blue; the factors for broadness are not limited, in the white as little as in the blue individuals. But it further becomes evident that complete independence of the colour and breadth is only superficial. In a certain sense there is indeed an interdependence between them, for the same factor C which is necessary for the occurrence of the blue colour. has a limiting action on the factors for broadness, and if the factor B alone were to disappear from the blue-flowering offspring, then on this account colour as well as breadth would change. The colour would then become white, because C alone cannot produce blue, and the breadth would be lessened under the influence of C alone. In this crossing the relationship is, however, so affected by the presence of B that the interdependence between the factors for broadness and colour is not noticeable and these characters behave independently. *It is therefore clear that when in a crossing two* characters behave quite independently we may not conclude, that an interrelation between the factors for these characters is wholly wanting.

In crossing common blue flax *AABBCC* with the narrow-petalled white *AACC,* which differ in breadth and in colour, a complete connection was observed between these two characters. All blue descendants had the broadness-type of the common blue flax, all white ones were of the narrow-type like the white *P*-variety. This is now also quite intelligible. It was shown above that the narrow-petalled white flax has the same factors for broadness as the common blue. All offspring from the crossing of these two varieties will therefore have the same factors for broadness. Now all the blue descendants possess, in addition to these factors for broadness also both the factors *B* and *C,* the white ones however have, besides the factors for broadness, only *C.* In all the blue therefore the factors for broadness are undisturbed, they will in consequence all have the breadth of the blue *P*-variety. In the white ones on the other hand the factors for broadness are inhibited, they will be narrow like the white *P*-variety. It follows that in this case also the interdependence between breadth and colour is other than can be deduced off hand from this crossing. The blue colour and the greater breadth of the common blue flax are not caused by the presence of a single factor or group of factors, in the absence of which the colour is white and the breadth smaller, but the relationship is a different one. The factor *B* which is present in the common blue flax, and absent from the narrow-petalled white, is not at the same time a factor for both, colour and broadness. In the two varieties there are present broadness-factors other than *B* and they are the same for both; but in the narrow-petalled white they are inhibited by *C,* in the common variety they are unaffected owing to the presence of *B* and *C* together.

Further the more complicated phenomena which were observed in the crossing between Egyptian *AABBCC* and the narrow-petalled white flax *AACC,* can now be completely explained. The difference between these two varieties is, so far as the factors for broadness are concerned, exactly the same as that between Egyptian and common blue and as that between Egyptian and common white flax. For the narrow-petalled white flax has the same factors for broadness as the common blue and the common white. Now since the broadness-factors follow the segregation law quite independently of the presence or absence of the factors *B* and *C,* the offspring will agree perfectly, as regards presence of broadness-factors, with the offspring from the crossings of the Egyptian flax with the common blue or the common white.

If no other causes were acting the individuals of F_2 would together show all transitions of breadth from the common blue or white flax to the Egyptian. Individuals with petals as narrow as those of the narrow-petalled white flax would not occur, for as has been shown, this variety agrees in factors for broadness with the common blue and common white flax. Moreover there would be no difference between the blue and the white. The phenomena are, however, altered by the presence of the factor C by itself or of the factors B and C together. The blue offspring possesses B as well as C, the inhibiting action of C is therefore removed and the blue individuals of F_2 must show all transitions from the breadth of the common blue or white to that of the Egyptian flax. The narrowest blue offspring cannot therefore agree with the narrow-petalled P-variety, but with the common blue or white flax, the broadest must agree with the Egyptian as has indeed been observed.

The white offspring of the crossing all possess the factor C only; the breadth in all individuals will therefore be less than if it were exclusively the result of the existing factors for broadness. They are not, however, all restricted to the factors for broadness of the narrow-petalled white flax, but some individuals even have the same factors for broadness as the Egyptian flax, others are intermediate with regard to the factors for broadness. Individuals, which have the same factors for broadness as the narrow-petalled white flax will agree also in breadth with this P-variety, because they, like it, have only the factor C. The individuals with the same factors for broadness as the Egyptian flax will, however, not have the type of broadness of this P-variety because of the presence of C, but they will be narrower. The white F_2-individuals together will show therefore a breadth ranging between the minimum of the narrow-petalled white and a breadth less than the maximum of the Egyptian flax. The aforementioned observations agree with this, the broadest white offspring from this crossing does not even reach the average of the Egyptian, hardly exceeds its minimum.

The behaviour also in the third and following generations is seen to be in agreement with what has been discussed. A heterozygotic blue plant of F_2, with petals 13 mm. broad, produced blue offspring with a breadth of 9.1 to 14 mm and white with a breadth of 7.1 to 11.1 mm. Another narrower, heterozygotic blue F_2-individual with a breadth of 9 mm. produced blue plants in F_3 of 7 to 10.7 mm. in breadth and white ones of 4 to 6.5 mm. The first broader F_2-plant had more factors for broadness than the second and this is also observable in the offspring, but in both cases the white F_3 is narrower as a result of the influence of C.

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The foregoing shows that all the phenomena observed in the different crossings are, without exception, completely explained by the action of the factors *B* and *C* in relation to the factors for broadness which are present. Another question now arises with reference to the strength of the inhibitory influence of *C*: it is the following. Does *C* exercise an influence on the factors for broadness occurring in the common blue or common white flax only or are the additional factors for broadness present in the Egyptian flax also subject to the inhibitory action of *C*? From the observations something indeed can be deduced with respect to this. The average breadth of the common blue flax is 7.0 mm. and of the common white 7.1 mm., whilst that of the narrow-petalled white is 3.3 mm. The breadth therefore is decreased from 3.7 to 3.8 mm. by the influence of *C*. Now in the crossing of the Egyptian flax with the narrow-petalled white the average breadth of 100 blue individuals in F_2 was 10.8 mm. and of 100 white 4.6 mm. That is a difference of 6.2 mm. Here, where the broadness-factors peculiar to the Egyptian flax are also present, the decrease in breadth caused by *C* is more marked. This is also evident from a comparison of the maximum that is reached by the white offspring of this crossing with the maximum of the Egyptian flax. The former amounts to 11.4 mm., the latter to 16.4 mm., that is to say there is a difference of 5 mm., a good deal more therefore than the diminution which the breadth of the common white flax suffers under the influence of *C*.

As other investigators have many times shown there occur in the plant not only factors which are quite independent of each other, but in many cases the perceptible action of one factor depends on the presence or absence of one or more other factors. It is even likely that no single factor is wholly independent of others, but that in many cases the factors only appear to be so, because in the investigation the two forms crossed, which are found to differ in respect of one given factor, are identical as regards other factors connected with that one. Thus, for instance, from the crossing of the common blue flax *AABBCC* with the common white *AABB*, it is only evident that the former has one factor more, than the latter, namely *C*, but not that this factor *C* is in a certain sense dependent on *B* and can only have an inhibitory action on the factors for broadness, if *B* is absent.

The present investigation shows that the factors may be mutually interrelated in a complicated way and may exercise an influence on each other. In the varieties of *Linum usitatissimum* which have been investigated, the factors which are present for the breadth of the petal are inhibited by another factor C, whilst again another factor B is able to counteract the inhibitory action of C; B is the inhibitory factor of the inhibitory factor C.

Because moreover the factors B and C together cause the blue colour of the flower, there arise complicated relationships with regard to the interdependence between the breadth and the colour of the petal.

There are various cases known of the existence of inhibiting factors, but so far as I know the existence of factors which are able to counteract the inhibitory action of inhibiting factors, has not hitherto been demonstrated.

It is moreover evident from this paper that the different mutual crossings of some varieties may lead to varying conclusions.

When only the crossing of the common blue flax with the narrow-petalled white was investigated, one would have come to the conclusion, that in the common blue flax the breadth and the colour are caused by the same factor or factors, or that the factors for these characters are completely coupled in these varieties.

Knowing only the observations on the crossing of the Egyptian flax with the common white, one would have concluded that the factors for the breadth and colour of the petal are completely independent of each other.

From the crossing of the Egyptian with the narrow-petalled white flax, without a knowledge of the results of the other crossings, one would, on the other hand, be obliged to postulate an interrelation between the factors for broadness and colour certainly insusceptible of further definition, whilst the factors for broadness apparently present here an exception to the Mendelian law of segregation.

From this it is seen that the phenomena are much more complicated than the two first-mentioned crossings by themselves give evidence of.

But at the same time the investigation of the different crossings together has proved, that, when two characters in the crossing behave quite independently, the inference cannot be drawn without further proof that there will also be no interrelation whatever between the factors which cause these characters.

The above clearly shows how relative our knowledge is. Views on the presence and action of factors obtained by an investigation of one single crossing, however simple and well founded they may be, are liable to modification when even only one of the forms investigated is crossed with a third form. Hence it is necessary to cross the same form with more than one partner in order to arrive step by step at the truth.

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