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ON THE RELATION OF HALF-HOARINESS IN MATTHIOLA TO GLABROUSNESS AND FULL HOARINESS.

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THE half-hoary Stock is not a type which one ordinarily meets with in cultivation, for the reason, perhaps, that it is not listed in seedsmen's catalogues. On this account it is somewhat difficult to procure, and one's stock once allowed to run out is not easily replenished. For this form is a perfectly distinct type, and though intermediate in character between the fully hoary and the glabrous condition it cannot be obtained by the simple process of mating these forms together[1]. It is possible that it is this form which is intended by Linnaeus[2], when he speaks of "*varietas alba nuda vixque tomentosa*," but as regards its origin we have, so far as I am aware, no information.

As is common knowledge the ordinary *fully* hoary Stock is everywhere densely covered with a tomentum of characteristically branched hairs: the vegetative axes, leaves, peduncles, pedicels, sepals and siliquae all exhibit a grey-white appearance due to the presence of these hairs. Further, in double-flowered plants there may even be a sprinkling of hairs on the outer surface of the petals. I have elsewhere pointed out that such a double flower as the Stock does not differ greatly from such a vegetative shoot as the Brussels Sprout. The persistence in the double Stock flower of the terminal growing point, the presence of numerous axillary buds among the petals and the occasional development within the flower of an internode of appreciable length (as much as a quarter to half an inch) show that here the flower

[1] Not, at least, such commercial forms as are at present available.

[2] *Species Plantarum*, 2nd ed. p. 925, 1762. There is no mention of this variety in the earlier edition (Holmiae, 1753).

shoot is far less profoundly modified than is the case with the single. In the presence of corolline hairs, which are not found in the single, even when hoary, we see the retention of yet another vegetative character.

The half-hoary type as well as the fully hoary was employed in the earliest stages of these investigations[1]. The strain then used was an annual white-flowered form which had been obtained together with some true *incana* from the Isle of Wight. It was ascertained that this half-hoary strain bred true and exhibited certain definite relations to the glabrous forms with which it was crossed. Unfortunately before these experiments were complete the half-hoary form was lost, and further investigation was held up for several years until a new half-hoary strain with pale purple (azure of commerce) flowers was by chance obtained. Being of slower growth, rather intermediate than annual in habit, this new strain was not so well suited for experiment as the one originally employed. In respect of surface character however the two types were precisely similar.

The distinctive feature of the half-hoary type is a certain definite localised inequality in the distribution of the hairs. The under surface of the leaves, the sepals and the pods are fully hoary. On the upper surface of the leaves the number of hairs is far fewer; the effect by contrast is to give a deceptive appearance of smoothness, although in fact this surface is thinly covered all over with hairs. The stem is for the most part actually glabrous, but as we pass up the shoot a certain overflow as it were of hairs from the leaf bases may give rise to decurrent hairy streaks which may become gradually more emphasised, until, in the shorter internodes of the flowering region, the glabrous area, in an extreme case, may be limited to the opposing (axillary) faces of the main axis (peduncle) and the pedicels. The partially glabrous habit readily distinguishes this from the fully hoary type.

In order to make clear the relations of the half-hoary form to the fully hoary and the glabrous types respectively it will be advantageous to restate briefly the position as to the relation in which these two latter types stand to one another. As we conclude, from the fact that some true-breeding *white* Stocks, when crossed, give rise to *coloured* offspring, that the combination of two factors (indicated by *C* and *R*) is required to produce colour, so the fact that it is possible to obtain a *hoary* F_1 from two coloured *glabrous* strains, or even from two individuals of the same coloured strain, leads us to assume the existence of

[1] See "Reports to the Evolution Committee of the Royal Society," *Report I*, p. 33.

two factors (indicated by *H* and *K*) which are necessary to produce hoariness. A further point, of special interest, is that the hoary character due to the presence together of *H* and *K* is not manifested *unless the colour factors C and R are also present*; that is to say, a plant may contain *H* and *K*, but if the flower is white (or cream) *owing to the absence of C, or R, or both*, it will not be hoary[1]. This curious interdependence between the hoary character and presence of sap colour in the flower is not confined to the ordinary garden varieties of Stocks. In *M. sinuata* one likewise meets with a hoary type and a glabrous variety (var. *oyensis*) in which loss of hoariness goes with loss of flower colour. The hoary type has pale purple flowers; in the glabrous plant the flowers are white. The two are recorded as growing associated together on the Île d'Yeu off the coast of La Vendée[2].

We may express the factorial composition of the hoary and glabrous types as follows:

(1) Hoary types will contain *C*, *R*, *H* and *K*.

(2) Coloured glabrous strains may contain *CRH*, *CRK* or only *CR*.

(3) White or cream glabrous strains may contain any of the following single factors or groups of factors, *C*, *R*, *H*, *K*, *HK*, *CH*, *CK*, *CHK*, *RH*, *RK*, *RHK*; or they may lack all.

Among glabrous types then, if *homozygous*, we shall have to consider 3 possible sap-coloured forms and 12 possible whites and creams. If interbreeding occurs giving rise to *heterozygotes* we shall expect a larger number still, as many in fact as there are combinations of these factors which do not involve the presence of all four, i.e. a total of 20 among sap-colours and 45 among the white and creams. Similarly in the hoary group, to the one homozygous form we should add 15 possible heterozygotes. The precise constitution of all these different forms has been set forth in detail in an earlier paper and need not be repeated

[1] The combination of hoariness and absence of any sap colour does however occur. We are familiar with it in the case of the white form of *incana* and in hoary white Brompton Stocks, but in these cases the white flower does not result from the *absence* of *C* or *R*. All the four factors *C*, *R*, *H* and *K* can be shown to be present; the absence of colour here must be ascribed to some other cause of the nature of inhibition. In Bromptons and some annuals the inhibition appears to be absolute, but in *incana* a noticeable tingeing of the flowers on fading affords further proof that the colour factors are not actually wanting. Whereas then in the *glabrous* whites one or both of the necessary factors for colour are absent, in *hoary* whites they are present but non-effective. It is only to the class of deficient whites (as opposed to inhibition whites) that the statement made in Punnett's *Mendelism* (3rd ed. p. 50) holds good, viz. "that in families where coloured and white Stocks occur the whites are always glabrous."

[2] See Curtis's *Botanical Magazine*, Vol. CXXVI. Tab. 7703, 1900.

here[1]. It will suffice to emphasise the fact that mere inspection of the individual in flower will not enable us to distinguish between the different forms included in any one of the three groups. There is nothing *visibly* different in the different classes of whites and creams; and among sap-coloured plants, individuals of the *same* colour and surface character *may* belong to any class within the group, or, on the other hand, plants of *different* colours (purple, red, flesh, etc.) *may* all belong to *one* class. The only method of identification at present available is the slow and laborious one of cross breeding, which necessitates the separate testing of each individual. The commercial material from which, from time to time, a fresh start had to be made was found to give very uniform results. Matings between hoary and glabrous types constantly gave all hoary[2] in F_1 and a mixed offspring in F_2 in the ratio of $3H : 1G$. When two glabrous forms were intercrossed a hoary F_1 was sometimes obtained in cases where both parents were non-sap-coloured, and again where one was sap-coloured and one not.

[1] "Further Contribution to the Study of Hoariness in Stocks (Matthiola)." *Proc. Roy. Soc.* B. Vol. LXXXV. 1912.

[2] During the progress of these experiments I have become convinced that when the hoary parent is homozygous this result invariably obtains. In the first set of experiments set out in *Report I* (*loc. cit.*) a certain number of cases are given in which glabrous individuals were recorded among the F_1 plants from the mating glabrous ♀ × hoary ♂ which, if genuine, suggested the possible occurrence of parthenogenesis. (See *Report I*, Table II. p. 38 and Table XIV. p. 83 in which the reference numbers of the particular experiments are quoted under "aberrant cases.") That these cases are *not* genuine exceptions and are *not* to be explained as due to parthenogenesis I now feel no doubt. I believe them to be due to the omission of some precaution which later experience led me to adopt, though I am still at a loss to suggest the particular cause of the experimental error.

The same remark applies to the case of *Salvia Horminum*. In the account of the investigations of the relations of the pink and white varieties to each other and to the violet type, which appears in *Report II*, two exceptions are recorded to the dominance of pink to white, and it is there suggested that these two exceptions may be due to experimental error. This we may safely hold to have been the case, for the factor relations in the case of Salvia are of the simplest type. The pink variety owes its colour to the presence of a factor P. The violet type contains the colour factor P and in addition a factor B which turns the pink colour blue. Whites lack the colour factor P and hence B which was present in the plants employed is ineffective. This view of the presence of a single colour-producing factor upon which another factor changing the class of colour may be superposed, which therefore regards the white as lacking this same colour factor rather than as containing a distinct factor W, leads us to expect the now familiar ratio $9V : 3P : 4W$ in F_2 from $P \times W$ (i.e. $bP \times Bp$) and not, as originally suggested, $2V : 1P : 1W$. The numbers actually recorded are, as will be seen on reference to the Tables, in closer agreement with the correct interpretation. The "presence and absence" view is now so familiar that this note would hardly have been called for were it not that no actual reference to this particular case putting it in line with many others happens to have been made in the course of the later work.

In every case such matings gave a proportion of hoary and smooth in F_2 approximating to $9H : 7G$. From these results it is clear that this commercial material consisted of pure (homozygous) forms and, further, that in the glabrous strains one was dealing solely with 3-factor forms (*CRH*, *CRK*, *CHK* and *RHK*). Starting with this material however it should be possible, according to the view here taken and in the absence of any indication of further complications due to coupling by appropriate matings, to eliminate successively *all* the different factors and to obtain the several simpler forms containing only 2 factors, 1 factor, or even none. From the new forms thus obtained a new set of ratios would of course result. We may state the expectation for the various cases in general terms thus:

When a hoary plant, however produced, is heterozygous in regard to any of the four factors *C*, *R*, *H*, *K*, it will yield a mixed offspring in which hoary individuals will predominate, *or* glabrous, according as the parent is heterozygous in one or two factors only, *or* in more than two. The ratio in the several cases will be as follows:

$3H$:	$1G$	if the parent is	heterozygous	in 1	of the 4 factors.	Excess of hoary
$9H$:	$7G$	,,	,,	2	,,	,,
$27H$:	$37G$	,,	,,	3	,,	Excess of glabrous
$81H$:	$175G$	,,	,,	4	,,	,,

In the earlier accounts of this work abundant evidence has been given of the occurrence of the ratios $3H : 1G$ and $9H : 7G$[1]. It remained to obtain similar proof that by a proper sequence of matings the simpler forms, presupposed by theory, could be obtained from the more complex: in other words to procure evidence of the actual occurrence of the ratios $27H : 37G$ and $81H : 175G$.

This has now been done. F_2 families bred from grandparents containing the required combination of factors have given excess of glabrous individuals in the expected ratios, as shown by the results given below.

A. Cases where the expectation is $27H : 37G$.

Form of mating		Result obtained in F_2		Expectation in F_2	
		Hoary	Glabrous	Hoary	Glabrous
CRHk	*cRhK*	37	49	36	50
crHK	*CRhK*	41	49	38	52
CrhK	*cRHK*	43	54	41	56
,,	,,	18	24	18	24
,,	,,	26	30	24	32
,,	,,	28	31	25	34
,,	,,	33	50	35	48

[1] See *Reports I, II* and *III*.

B. Cases where the expectation is $81H : 175G$.

Form of mating		Result obtained in F_2		Expectation in F_2	
		Hoary	Glabrous	Hoary	Glabrous
CRHk	*crhK*	17	33	16	34
,,	,,	67	135	64	138

The agreement between expectation and the results actually obtained is sufficiently convincing. If these same F_1 crossbreds are crossed back with a glabrous type instead of being self-fertilised, another series of ratios is obtained. The F_2 ratio in these cases depends upon how many of the 4 factors have been introduced into the pedigree *more than once* in the course of the two matings. We may state the results of the various possible combinations in general terms as follows:

	Various ratios obtainable in F_2 when a hoary F_1 crossbred is bred back with a glabrous type	Conditions under which these different ratios are obtained
(1)	$1H : 1G$	if 3 out of the 4 factors be introduced more than once
(2)	$1H : 3G$	if 2 out of the 4 factors be introduced more than once
(3)	$1H : 7G$	if 1 out of the 4 factors be introduced more than once
(4)	$1H : 15G$	if none out of the 4 factors be introduced more than once
(5)	all H	if each of the 4 factors be introduced more than once

Since in the early experiments, one case excepted, only 3-factor glabrous types were available, viz. *CRH*, *CRK*, *CHK*, *RHK*, the results obtained from breedings in the form heterozygous hoary × glabrous all fall into either the first or last category given above. As, by suitable breeding, material in which the several factors have been eliminated is obtained, the ratios with the higher proportions of glabrous to hoary can be shown to occur. This has already been done in case (2). From a breeding of the form $(CK \times RHK) \times CK$ in which the F_2 expectation is $1H : 3G$, two F_1 plants yielded respectively

$$8H : 23G,$$
$$1H : 3G.$$

To obtain the two higher ratios $1H : 7G$ and $1H : 15G$ is merely a question of further elimination, identification, and suitable mating.

We may therefore regard the conclusions formulated in the earlier paper quoted above[1] *as fully established.* Stated in the briefest possible way they amount to this: *That the inter-relations of the fully hoary and the glabrous types depend upon two pairs of factors (indicated by CR and HK) which segregate in the normal way, the one pair being essential for the production of sap-colour, the other for hoariness, the latter pair*

[1] See note 1, p. 148.

being however non-effective unless combined with the former. Having brought our consideration of the inter-relations of hoary and glabrous to this point, we can now proceed to consider the relations of these types to the half-hoary form.

The characteristic features of the half-hoary form have been described above (p. 146). It may be added that this type is peculiar in that the adult appearance is not assumed from the beginning as is the case with the fully hoary and glabrous types. As a rule the first leaf after the cotyledons has only quite a few hairs on the basal and extreme apical margins. The succeeding leaves exhibit an increasing degree of hairiness until about leaf 5 when the half-hoary condition is generally reached and thenceforward maintained, except that in the axillary buds a similar grading may be repeated, one or two of the first young leaves, especially if rather stunted, being very slightly hairy, the succeeding ones typical. In this behaviour we are reminded of another Crucifer, *Biscutella laevigata*, in which hairy, intermediate and glabrous forms are found. In *Biscutella* as in *Matthiola* transition stages from a juvenile to a stable adult condition—stages which may sometimes be witnessed again in an axillary shoot—commonly occur in the intermediate plants, but in the case of *Biscutella* the gradation is from the partially hoary towards the glabrous condition; in the half-hoary Stock it is in the opposite direction—towards the fully hoary condition[1]. This return in the axillary shoot to a grade represented at a lower level on the main axis is curious but not uncommon in plants. It is not confined to the period of vegetative development; it may equally be observed in flowering shoots as, e.g., in *Digitalis purpurea* var. *heptandra* and in *Erodium pimpinellifolium*. In *D. heptandra* as described elsewhere[2] there is a gradual transition up the spikes from a more extreme heptandrous condition towards the normal until the end of the flowering season when the flowers often show a slight retrogression towards the abnormal condition. In the axillary shoots the starting-point is usually some intermediate stage in the series—one which has already been passed through by the main axis at the time that the axillary shoot begins to flower.

In *Erodium pimpinellifolium* the flower is commonly described as having the two postero-lateral petals distinguished from the other three

[1] Fuller details are given in an account of observations "On a discontinuous variation occurring in *Biscutella laevigata*," *Proc. Roy. Soc.* Vol. LXII.

[2] "On Inheritance of a Mutation in the Common Foxglove (*Digitalis purpurea*)," *The New Phytologist*, Vol. x. 1911, p. 54.

by the presence of a basal area or spot of a different colour from the rest of the petal, being thus distinguished from the nearly allied *E. cicutarium* in which all five petals are alike and unspotted. If however the flowers of *E. pimpinelli/olium* are recorded during a season, it will be found that occasionally the earliest flower has all five petals spotted, though I do not think I have ever observed more than one flower of this type on an axis, and even one is not very common. One or two succeeding flowers may show four petals spotted, occasionally one may follow with three spots, and then the plant settles down to the 2-spot pattern until the close of the flowering season when a downgrade series begins once more, the spots diminish in size until in the last flowers they often cannot be detected at all. The point of interest is that the earlier lateral axes also often produce at first a few flowers with more than two petals spotted, although the first flowering stem may have already passed on to the stage of producing only the 2-spot flowers. We do not as yet understand the causes operating in these cases, and a statement of the facts is all that is possible.

The inter-relations existing between the half-hoary Stock and the glabrous or fully hoary types are especially interesting as they reveal to us for the first time a difference in the relations of the two factors *H* and *K* to a third factor. Hitherto in absence of evidence to the contrary these two factors have appeared to stand in a complementary but equivalent causal relation to surface character. Results obtained from any series of matings involving the presence of *H* but not *K* could equally be obtained by using the corresponding forms containing *K* but not *H*, provided that the substitution of *K* for *H* in these operations was made throughout. Such is not the case when the half-hoary form is employed in these matings, and it is from the use of this type that we obtain the first piece of evidence that the *rôle* played by one factor of the *HK* pair is different from and not merely complementary to that of the other.

The results of various matings in which this type was employed are set forth below (p. 153).

The condition here designated as quarter-hoary is quite definite, and the individual exhibiting this character has a definite constitution and behaviour. As regards appearance the quarter-hoary plant is at first completely glabrous, but in the later stages of development leaves are produced with marginal hairs, or with even a few on the surface. Scattered hairs may be present on the ab-axial side of the pedicels and a fair number occur on the basal region of the sepals, although not

Results obtained in F_1 when a coloured half-hoary form was bred with fully hoary or glabrous types.

Expt.				
(1)	Hoary white (*incana*) (*CRHK*)	× ½ hoary	F_1 all hoary	(10 plants)
(2)	Glabrous coloured (azure) (*CRH*)	× ,,	F_1 ,,	(10 ,,)
	Reciprocal mating with flesh (*CRH*) instead of azure	× ,,	F_1 ,,	(1 ,,)
(3)	½ hoary × glabrous sulphur-white (*RHK*)		F_1 ,,	(21 ,,)
(4)	Glabrous coloured (marine) (*CRK*)	× ½ hoary	F_1 all ¼ hoary	(56 ,,)
	Reciprocal mating		F_1 ,,	(10 ,,)
(5)	Glabrous white (*CK*)	× ,,	F_1 ,,	(3 ,,)
	Reciprocal mating			(7 ,,)
(6)	Glabrous sulphur-white (*CK*)	× ,,	F_1 ,,	(5 ,,)

Results obtained in F_2 from the matings mentioned above.

(*a*) *From F_1 × self*

Expt.	Parents		F_2 Hoary	Half-hoary	Quarter-hoary	Glabrous
(7)	½ hoary × glabrous flesh (*CRH*)	$F_1 = H$	19	7	1	17[1]
(8)	,, × glabrous sulphur-white (*RHK*)	$F_1 = H$	41	13	3	3[1]
(9)	Glabrous marine (*CRK*) × ½ hoary	$F_1 = \frac{1}{4}H$	—	181	$297+x$	$163+y$
(10)	,, sulphur-white (*CK*) × ½ hoary	$F_1 = \frac{1}{4}I$	—	2	4	1
(*b*)	*From F_1 × a glabrous type*					
(11)	[½ hoary × flesh (*CRH*)] × flesh (*CRH*)		14	—	—	13

$x+y=70$. See reference in text.

Results obtained in F_3 from the self-fertilisation of F_2 individuals obtained in Experiment 9.

Expt. 12. 8 F_2 half-hoary individuals self-fertilised yielded only half-hoary offspring (88, 63, 27, 37, 54, 59, 45, 27, respectively, making a total of 400).

Expt. 13. 3 F_2 glabrous individuals self-fertilised yielded only glabrous offspring (17, 38, 34 respectively, making a total of 89).

Expt. 14. 9 F_2 quarter-hoary individuals yielded a mixture of the three forms as follows:

	Half-hoary	Quarter-hoary	Glabrous or quarter-hoary	Glabrous
(1)	26	41	10	20
(2)	18	29	5	15
(3)	11	13	2	4
(4)	32	38	5	27
(5)	9	34	7	13
(6)	8	14	7	3
(7)	—	2	—	1
(8)	3	3	1	7
(9)	14	24	8	4
Totals	121	$198+x$	$x = \leftarrow 45 \rightarrow = y$ $(=x+y)$	$94+y$
Expectation	$114\frac{1}{2}$	229	—	$114\frac{1}{2}$

[1] In experiments 7 and 8 such a large proportion of the seeds failed to germinate that a wider deviation from the expected numerical result than one would ordinarily anticipate may well occur. For the expectation in these cases see p. 157.

always in the earliest flowers. The siliqua is distinctly hairy though less so than in the half-hoary type. The stem is glabrous in the flowering as well as in the vegetative region. The appearance of the siliqua furnishes the readiest means of recognition; doubles are consequently less rapidly identified, the leaves and sepals often requiring close examination. Exceptionally, one may meet with quarter-hoary individuals showing in some limited area or member a total absence of hairs; in one plant, e.g., the second siliqua in the raceme was quite glabrous although all the others showed the quarter-hoary condition; in another the two surfaces of one siliqua were sharply differentiated, the one component carpel being characteristically hairy, the other quite glabrous. Such 'mosaic' cases are however distinctly rare. *As regards behaviour and constitution the quarter-hoary individual is a heterozygote incapable of breeding true since it forms no gametes corresponding to the appearance of the zygote.* It is comparable with the classic case of the Blue Andalusian among fowls, and like its animal counterpart yields always a proportion of one of each of the parental forms from which it is derived to two of itself, the parental types breeding true, the heterozygous form yielding again this same proportion in succeeding generations. This behaviour is clearly proved by the results recorded above in F_2 (Experiments 9 and 10) and in F_3 (Experiments 12, 13, 14). In Experiment 9 where the total obtained from the quarter-hoary F_1 was 711 the expectation based on a ratio of $1G : 2\ \frac{1}{4}H : 1\ \frac{1}{2}H$ is

178 glabrous,
356 quarter-hoary,
178 half-hoary.

The record actually made showed

163 undoubtedly glabrous.

70 glabrous or quarter-hoary. From these 70 plants no record was obtained from the calyx and ovary, it is therefore uncertain how many of these originally glabrous plants really belonged to the smooth class and how many should be added to the quarter-hoary.

297 quarter-hoary.

181 half-hoary.

There is little doubt that, had the 70 plants which were classified only on the early vegetative character reached the flowering stage, the agreement between the observed and the expected results would have been extremely close, as it is in Experiment 10, despite the very small number recorded. The same may be said in regard to the numbers

obtained in F_3. The mixed offspring from the quarter-hoary F_2 plants occur in such proportions that we can hardly doubt that, had the 45 individuals which died early lived to maturity, the number to be added from the doubtful column to the quarter-hoary and glabrous classes respectively would have brought the totals into close agreement with expectation. As was anticipated all the glabrous and half-hoary individuals that were tested bred true.

The above series of results forms a concordant whole and gives us a new insight into the relations of the factors determining surface character. Taken in conjunction with what we already know they are explained on the following simple scheme:—

(1) That the half-hoary type lacks *H* but contains *K* together with an additional factor (indicated by *J*) which reacts with *K* to produce a certain degree of hairiness but definitely less than that exhibited by the fully hoary type.

(2) That when the amount of the dose, if we may so express it, of *J* is equal to that of *K*, *H* being absent, the result is the condition termed half-hoary, as seen in the half-hoary type employed which we may write *CRJK*.

(3) That when, on the other hand, one dose of *J* goes with a double dose of *K*, *H* as before being absent, as we have in the matings marine (*CRK*) × half-hoary, white (*CK*) × half-hoary and sulphur-white (*CK*) × half-hoary (see Experiments 4, 5 and 6), the result is to dilute the effect of *J* and to produce the quarter-hoary condition.

(By analogy it would be natural to suppose that in the converse case where the dose of *J* is double that of *K*, i.e. in the combination *JJKk* instead of *JjKK*, the individual would be intermediate in hairiness between the half-hoary and the fully hoary state, or three-quarter-hoary. The only mating among those given above which would produce this particular combination in F_2 is *CRJK* × *CRH* (half-hoary × glabrous flesh) which gave F_2 as shown in Experiment 7. As the expectation in this case would only be 1 three-quarter-hoary individual in 32 the fact that none were recorded among the 44 plants actually raised must not be regarded as conclusive evidence that a three-quarter-hoary form recognisably distinct from the half-hoary and the fully hoary does not exist. For the present this point must remain undecided. We may however go so far as to predict that whatever the *appearance* of individuals of the composition *CRJKCRJk* they will in *behaviour* resemble the quarter-hoary form in that they will not breed true owing to the non-existence of a gamete corresponding to this form of zygote.)

(4) That when the *JK* pair is combined with *H*, the colour pair *CR* being also present, the full degree of hoariness due to the combination *CRHK* masks the presence of *J*.

Whether the combination *JK* produces the half-hoary condition in *all* cases when *H* is absent, i.e. whether *J*, unlike *H*, reacts with *K* quite independently of *C* and *R*, has yet to be determined. The half-hoary type used in the present experiments being azure in colour obviously contained *CR*. The form originally used in the earliest experiments had indeed white flowers, but the absence of colour must be attributed to inhibition not to the absence of either *C* or *R*. For this half-hoary white gave all hoary in F_1 when crossed with either *CRH* or *RHK* whites and creams. Hence we must conclude that it contained both *C* and *R* and belonged to the class of inhibition whites referred to above (p. 147). Thus in neither case can we tell whether *J* would have been effective if either *C* or *R* had been lacking. Until a half-hoary white has been found or made which can be shown to belong to the class of defective whites this question must be left undecided. So far such a small number of extracted half-hoary plants have been flowered in matings which could yield the required combinations that the fact that those that were recorded were all coloured leaves the point still in doubt. Where a half-hoary type is crossed with a glabrous type, whether coloured or not, which lacks both *H* and *K*, we may however venture to predict that the *JK* pair brought in by the one parent will be effective and that the F_1 will be all half-hoary. With a half-hoary type therefore we are not able to predict as with a fully hoary type the result in F_1 when the mating is with a glabrous type of unknown composition. The fully hoary gives *always* fully hoary in F_1 whatever the composition of the glabrous parent as regards the factors *CRHJK*. The half-hoary, whether coloured or a white of the inhibition class, gives (1) fully hoary, (2) half-hoary or (3) quarter-hoary according as the glabrous type (1) contains *H* either with or without *J* and *K*, (2) lacks all the three factors *H*, *J*, *K*, or (3) contains *K* but not *H* or *J*. To these three cases we may even need to add a fourth. For if the glabrous parent contain *J* without either *H* or *K*, it is quite probable that the F_1 will be a form (three-quarter-hoary) recognizably distinct from both the half-hoary and the fully hoary.

The results recorded above being capable of interpretation on the scheme of inter-relations between the factors as here stated, we may turn back for a moment to a consideration of the results recorded in

the earlier experiments[1]. At that time the fact that the adult condition was not assumed by the partially hoary plants in the early seedling stage, and in the case of the quarter-hoary plants not until quite late on, was not fully appreciated. Moreover the experiments were carried out on a considerable scale, and limits of space compelled one to discard large numbers of individuals in the seedling stage. It is owing to this circumstance without doubt that the quarter-hoary condition was only recorded in a single individual. For the same reason it is more than probable that in many cases a number of half-hoary plants discarded at an early stage will have been wrongly classified as glabrous. If these points are borne in mind together with the explanation offered above (see note, p. 148) of the false appearance of parthenogenesis in one or two cases, the results in which some discrepancy appears to exist between observation and expectation, based on the conclusions formulated above, all fall into line, and the whole series of earlier and later experiments taken together form a concordant whole which can be simply accounted for on the supposition of certain inter-relations between various pairs of factors as set out in the present account. For convenience of reference these earlier results are restated here together with the expectation which the later work now enables us to give for the various matings which have so far been carried out.

Expectation in the case of various matings of a half-hoary type, whether a white by inhibition or having coloured sap, with fully hoary and glabrous types.

	Mating	Expectation in F_1	Expectation in F_2				
			Hoary	Individuals containing *JJK*. Appearance not yet ascertained	Half-hoary	Quarter-hoary	Glabrous
(*a*)	$\frac{1}{2}H \times$ *Hoary*						
	$\frac{1}{2}H \times CRHK$	all H	12	—	1	2	1
(*b*)	$\frac{1}{2}H \times$ *Glabrous*						
	$\frac{1}{2}H \times CRH$	all H	36	2	5	2	19
	$\frac{1}{2}H \times CRK$	all $\frac{1}{4}H$	—	—	1	2	1
	$\frac{1}{2}H \times CR$	all $\frac{1}{2}H$	—	2	5	2	7
	$\frac{1}{2}H \times RHK$ / $\frac{1}{2}H \times CHK$	all H	36	—	7	14	7
			or 36	—	3	6	19
			if *J* proves not to be effective in the absence of *CR*[2]				
	$\frac{1}{2}H \times CR$	all $\frac{1}{4}H$	—	—	1	2	1
			or —	—	3	6	7
			if *J* proves not to be effective in the absence of *CR*[2]				

[1] *Reps. Evol. Ctee.*

[2] The considerable difference in the expectation as to glabrous plants in the two cases should make it easy to decide this point when once a full count has been obtained in F_2.

Conclusion.

The results recorded here and in the earlier work form a concordant body of facts concerning surface character which the scheme of factor relations here suggested enables us to bring together into a comprehensible whole. These factor relations involve five factors—*C*, *R*, *H*, *J*, *K*—inter-acting as three distinct pairs.

(1) The pair *CR* essential to the production of sap colour.

(2) The pair *HK* producing the fully hoary condition but only effective when the *CR* pair is also present.

(3) The pair *JK* which produces a less degree of hairiness than *HK*. For this reason the presence of *J* can only be detected in the absence of *H*. The effect of the combination *J* and *K* is to produce the condition known as half-hoary if the individual has the constitution *JJKK* or *JjKk*, i.e. if the dose of the two factors is equal. If *K* has been brought in on both sides of the pedigree and *J* only on one, i.e. if the individual has the constitution *JjKK*, the result is to dilute the effect of *J*, and the individual exhibits the lesser degree of hairiness known as quarter-hoary. It remains to determine the appearance of the individual in the reverse case when the constitution is *JJKk*, and also to ascertain whether the effect of *J* is independent of *C* and *R* or whether, like *H*, it is only effective when the colour pair is also present.

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