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THE INHERITANCE OF A RECURRING SOMATIC
VARIATION IN VARIEGATED EARS
OF MAIZE¹

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INTRODUCTION

THE inheritance of variegation has special interest and importance in genetics. It is with forms of variegation that the only two certainly known cases of non-Mendelian inheritance have had to do. I refer to Baur's experiments with *Pelargonium*, in which crosses of green-leaved and white-leaved forms exhibited somatic segregations in F_1 that bred true in later generations, and to Correns's work with *Mirabilis*, which showed green and white leaf color, to be inherited through the mother only. De Vries's conception of "ever-sporting" varieties was apparently founded largely upon the behavior of variegated flowers in pedigree cultures, from which he reached the conclusion that the variegated color pattern and the monochromatic condition arising from it as sports are non-Mendelian in inheritance. Correns, however, has shown that in *Mirabilis jalapa* the inheritance of these sports is distinctly Mendelian, and the results of East and Hayes indicate the same for *Zea mays*. In this paper I shall present data from maize and attempt to show how they can be interpreted in strictly Mendelian terms.

Variegation is distinguished from other color patterns by its incorrigible irregularity. It is perhaps most often seen in the coloration of flowers and leaves but also occurs in fruits, seeds, stems, and even roots of various plants. It is characteristic of the ears of certain varieties of maize known, at least in the Middle West, as "calico" corn. In

¹ The experimental results reported here were presented at the Cleveland meeting of the American Society of Naturalists, January, 1913. Research bulletin No. 4 of the Nebraska Agricultural Experiment Station.

these varieties the pericarp of most of the grains has few to many narrow stripes of dark red, the remaining area being colorless or showing a sort of washed-out red. Often broad red stripes appear on some grains, a single stripe covering from perhaps one tenth to nine tenths of the grain. Not uncommonly there are entirely colorless grains (so far as pericarp is concerned) and also solid red grains scattered over the ear. Much more rarely there is found a "freak" ear with a large patch of self-red or nearly self-red grains. Or sometimes an ear is composed largely of red or almost red grains with a small patch of striped or nearly colorless grains. In such cases it is not uncommon for the margin of the red area to cut across a grain so that one side—always the side toward the red patch—is red and the other side colorless or striped. Ears that are colorless throughout, except for a single striped grain, are not unknown and there are even known ears that are red except for a single striped grain. Very rarely a plant has one self-red ear and one variegated ear on the same stalk. It is also conceivable that all the ears of a plant might thus become red, but of course such a red-eared plant rising as a bud-sport could not ordinarily be distinguished from a red-eared plant arising as a seed-sport.

Variegated ears generally have variegated cobs, the amount of red in the cob ordinarily varying with the amount of red on the grains. In some "freaks" a part of the cob is solid red and the rest variegated. In a few such cases the red part of the cob corresponds exactly in position to the freak patch of grains. This is more frequently true when the grains of the freak patch are dark variegated than when they are self-red. In other ears there is no change in the cob corresponding to the change in the grains. The husks of variegated ears are also rather commonly variegated. In a few freak ears the red side of the ear is enclosed in reddish husks, the remainder of the husks being light striped. Red-eared plants arising as seed-sports always have solid red cobs and usually solid reddish husks.

The first account, so far as I am aware, of the inheritance of the striking somatic variations so commonly found in variegated plants was given by de Vries² in his discussion of ever-sporting varieties. The study was made in the years from 1892 to 1896 with a variety of *Antirrhinum* with striped flowers. De Vries's records are reproduced diagrammatically in Fig. 1.

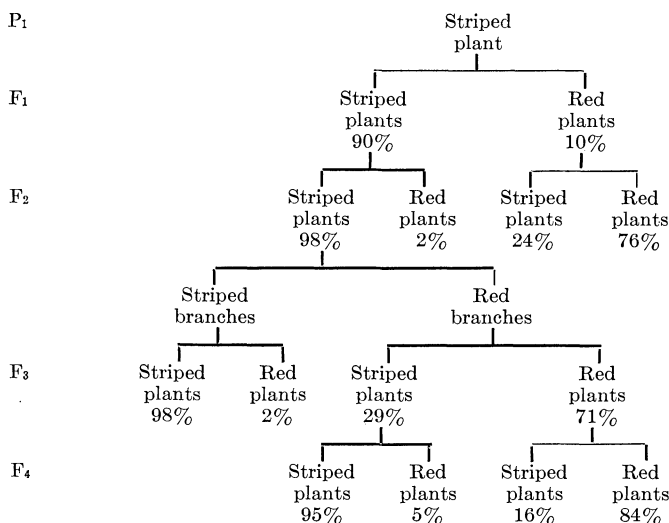


FIG. 1. DIAGRAM FROM DE VRIES'S RECORDS SHOWING THE INHERITANCE OF VARIEGATION AND SELF-RED IN THE FLOWERS OF *Antirrhinum*.

Of these results de Vries says:

From these figures it is manifest that the red and striped types differ from one another not only in their visible attributes, but also in the degree of their heredity. The striped individuals repeat their peculiarity in 90–98 per cent. of their progeny, 2–10 per cent. sporting into the uniform red color. On the other hand, the red individuals are constant in 71–84 per cent. of their offspring, while 16–29 per cent. go over to the striped type. Or in one word: both types are inherited to a high degree, but the striped type is more strictly inherited than the red one.

De Vries's results were in some respects very similar to those of Correns and it is probable that he would have interpreted them in the same way had he then been familiar with Mendelian phenomena.

² Vries, Hugo de, "Species and Varieties," pp. 309–328 (1905).

Correns³ has reported results of a careful study of the inheritance of the self-green condition appearing as a bud-sport on variegated-leaved plants of *Mirabilis jalapa*, and also of a self-color appearing in striped-flowered plants of the same species. His results for self-green and variegation of the leaves are shown diagrammatically in Fig. 2. The results are stated in approximate percentages. I have seen no report in which the detailed records were given.

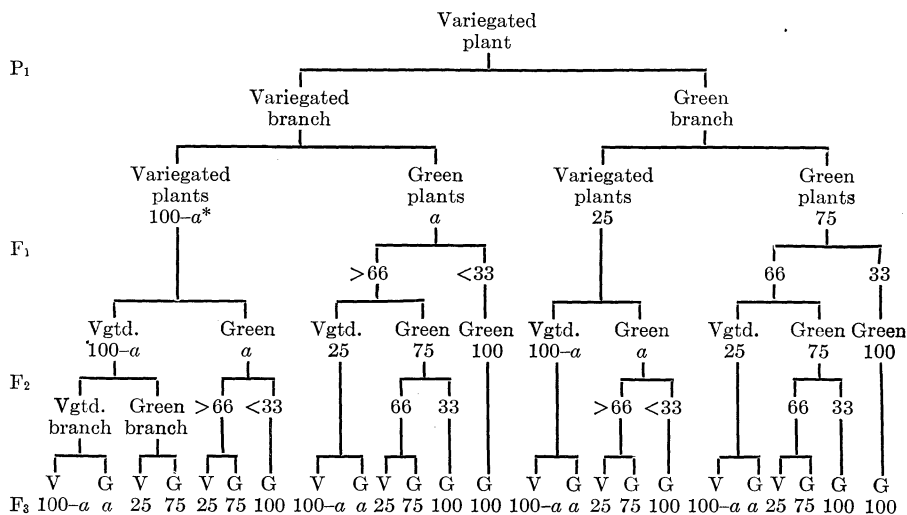


FIG. 2. CORRENS'S DIAGRAM SHOWING THE INHERITANCE OF VARIATION AND SELF-GREEN IN THE LEAVES OF *Mirabilis jalapa*.

The diagram shows that a variegated branch of a variegated plant produces in F₁ mainly variegated plants, but occasionally a wholly green plant, while a green branch from the same plant produces in F₁ 25 per cent. variegated and 75 per cent. green plants. The F₁ variegated plants, however produced, behave in later generations just like the original variegated parent plant. The F₁ green plants, whether produced from green or variegated branches, are always of two sorts, namely, those that are homozygous and therefore breed true green, and those

³ Correns, C., *Ber. Deutsch. Bot. Gesel.*, 28: 418-434, 1910. *Der Übergang aus dem homozygotischen in einen heterozygotischen Zustand im selben Individuum bei buntblättrigen und gestreiftblühenden *Mirabilis*-Stippen.*

* Numerals indicate approximate percentages; a = 0-10 per cent.

that are heterozygous and therefore produce progenies of green and variegated individuals in a ratio of approximately 3 to 1. Correns points out that a green branch of a variegated plant behaves as though it belonged not to a variegated plant at all, but to a hybrid between a variegated plant and a green one, in which green is dominant, and that half of the germ cells produced by the green branch carry a factor for green and the other half a factor for variegation. Similar results were secured from branches with self-colored flowers on plants with striped flowers, except that such branches produce few if any more self-colored plants than are produced by branches with striped flowers. Plants with self-colored flowers, no matter how they arise, behave as they would if they had occurred in an F_2 progeny of a cross of striped by self-colored plants.

RESULTS OF EXPERIMENTS WITH MAIZE

Hartley⁴ in 1902 gave an account of an experiment with variegated maize. In a comparatively pure white strain, which occasionally produced a red ear, there was found an ear similar to some of the "freak" ears noted earlier in this paper. It is described as being red except for a spot covering about one fifth of the surface, in which the grains were white with fine red streaks. The excellent plate accompanying the account, however, shows that most of the "red" grains had white streaks at the crown and that the cob was light-colored, not red. From the near-red grains of this ear there was produced a crop of 84 red ears and 86 pure white ones, while from the variegated grains of the same ear there came 39 light variegated ears and 36 white ones. Hartley refers to the parent ear as a "sport or sudden variation from the type" but does not indicate whether the "type" in mind was the white variety or the red ears occasionally produced by it. Both the color of the grains and cob and the production of about 50 per cent. of white ears from both the red and the variegated grains indicate very clearly that the parent ear was a

⁴ Hartley, C. P., Yearbook, U. S. Dept. Agr., 1902: 543-544.

heterozygous, variegated one and that it probably came from a white seed crossed by a stray grain of pollen from a variegated-eared plant, just as the occasional red ears in the white variety were certainly produced by stray pollen from red-eared plants.

More recently East and Hayes⁵ reported like behavior of a similarly variegated ear. An ear having on one side solid red grains and on the other white and very light variegated grains, similar to some of the "freak" ears noted earlier in this paper furnished the material for the test. The ear was produced from a white seed in a field of otherwise pure white corn and was therefore doubtless heterozygous for pericarp color and was probably pollinated in large part from plants without pericarp color, so that 50 per cent. white-eared plants were to be expected in its progeny. The white, the light variegated and the solid red grains were planted separately. The white and the variegated seeds alike produced light variegated and white ears, 15 of the former and 15 of the latter. The red seeds produced 22 white ears and 22 solid red ears. The authors' interpretation of these results is that the white seed which gave rise to the original colored ear had been fertilized by pollen from a red-eared plant and that the F_1 plant, "due to produce a red ear varied, somatically so that one half of the ear was red and one half striped." The authors further state:

This variation was transmitted by seeds, but at the same time the hybrid character of its seeds was unchanged as shown by their segregation into reds and whites in the next generation and the normal segregation of the hybrid dark reds in a further generation.

In the light of my own observations, it is equally possible and seems more likely that the white seed from which the original red-and-variegated ear came was the result of pollination from a plant with variegated ears, and that the somatic variation was from variegated grains to solid red grains rather than from red to variegated. But the important fact is that a somatic variation was later inherited in a strictly Mendelian way.

⁵ East, E. M., and Hayes, H. K., *Bul. Conn. Agr. Expt. Sta.*, 167: 106-107, 1911.

In 1909 I obtained results somewhat similar to those reported by East and Hayes. A few "freak" ears were secured, mainly from local and national corn expositions. Nothing was learned as to their parentage or pollination. Obviously, however, the parentage of the red, the variegated, and the white grains of any one ear was the same, and it is reasonable to suppose that the different sorts of grains of any one ear were pollinated with approximately the same kind or the same mixture of pollen. The results, as shown below, were essentially like those of Hartley and of East and Hayes.

Seeds Planted	Number of Plants with		
	Red Ears	Variegated Ears	White Ears
Self-red	43	0	33
Variegated and white	0	22	29

The results from four other ears were somewhat different, probably owing to differences in their pollination. (See Fig. 3.) They were as follows:

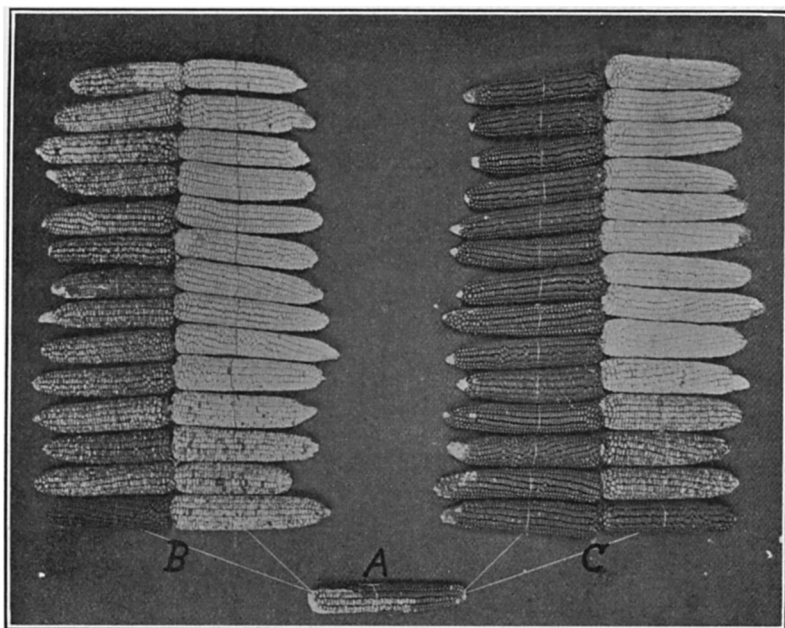


FIG. 3. A, "freak" ear of maize; B, progeny of striped seeds; C, progeny of self-red seeds.

Seeds Planted	Number of Plants with		
	Red Ears	Variegated Ears	White Ears
Self-red.	128	32	69
Variegated and white.	8	103	68

Two other ears of similar history, while they gave quite as striking results as those noted above, probably do not belong here since none of their immediate progeny were variegated and no variegated ears have occurred in later generations. These two ears were made up of red grains and white grains only. The results were as follows:

Seeds Planted	Number of Plants	
	Red Ears	White Ears
Red.	77	85
White.	0	122

The white ears bred true in later generations and the red ears produced reds and whites in typical Mendelian fashion. No such somatic variations as these have occurred in my cultures of self-red or white maize, so that I have been unable to study them further. Somatic variations in variegated corn, however, are not rare. Unfortunately several of the most pronounced of those occurring in my cultures were open-pollinated and therefore of little or no use in a careful study. I have therefore been obliged to make use in large part of the few solid red and nearly solid red grains scattered over otherwise more or less evenly variegated ears.

From twenty-three self-pollinated, variegated ears of plants that were homozygous for pericarp color, grains with various amounts of red were selected and planted. The results are summarized as follows:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears
Self-red.	8	9	0
Nearly self-red.	56	16	0
More than half red.	9	34	0
Less than half red.	5	22	0
Narrow red stripes.	33	394	0
Non-red.	1	22	0

Besides these 23 ears, 20 other selfed ears from homozygous plants contained only narrow-striped seeds from which there were produced 16 plants with red ears, 280 with variegated ears, and none with white ears. Similarly 21 selfed ears with narrow-striped seeds only, from plants that were heterozygous for pericarp color, produced 28 plants with red ears, 411 with variegated ears, and 208 with non-red⁶ ears. Various colored grains from 42 self-pollinated, heterozygous, variegated ears gave the following results:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red ⁷ Ears
Self-red	15	1	6
Nearly self-red	17	8	8
More than one half red	46	51	31
Less than one half red	8	34	21
Narrow red stripes	57	767	300
Non-red	0	10	6

In the progenies of these 63 self-pollinated ears that were heterozygous for pericarp color, there were approximately 2.5 plants with pericarp color to one without it. All the classes of grains from self-red to non-red yielded both colored and non-colored ears, thus indicating, as already shown by East and Hayes, that the somatic variation in the seeds does not change their hybrid character. Considering only the plants with pericarp color, in the progenies of both heterozygous and homozygous variegated ears, 106 progenies in all, marked differences are seen in the percentages of self-red ears from seeds of the different color classes, as follows:

⁶ Some of these ears had what I have termed "half-red" pericarp, *i. e.*, pericarp with a reddish color extending part way from the base to the crown of the seeds. (See Ann. Rpt. Nebr. Agr. Expt. Sta., 24: 62. 1911.) Half-red differs from self-red and variegated red not only in distribution but also in almost never developing fully in the heterozygous condition. It is hypostatic to self-red, but shows between the red stripes of variegated seeds. Since its presence does not mask either self-red or variegated-red and since it is strictly allelomorphic to both of them, half-red is here included with non-red. Variegated ears have never, in my observation, produced half-red grains as somatic variations.

⁷ Some of these were half-red. See footnote 6.)

Seeds Planted	Number of Plants with		Per Cent. Self-red Among Colored Ears
	Self-red Ears	Variegated Ears	
Self-red.....	23	10	69.7
Nearly self-red.....	73	24	75.3
More than one half red.....	55	85	39.3
Less than one half red.....	13	56	18.8
Narrow red stripes.....	134	1,852	6.7
Non-red.....	1	32	3.0

In comparison with the cases reported by Hartley and by East and Hayes and one of my first cultures from open-pollinated ears, in all of which red grains produced no variegated ears and striped grains no red ones, the striking features of the results from these 106 self-pollinated ears are the facts that the wholly red grains yielded some variegated as well as red ears and that the striped grains and even the wholly non-red grains yielded some red as well as variegated ears. The percentages noted above indicate in a general way that for self-pollinated, variegated ears, *the more red there is in the seed planted the larger the percentage of red ears in the progeny*. These records, however, do not give a wholly trustworthy indication of the mode of inheritance of the somatic variations concerned here. If there is a modification of some factor in the female gametes, associated with a visible modification of somatic cells of the pericarp and even at times of the cob and husks, modifications that do not become visible until long after the gametes are formed, may there not be a similar modification of the same factor in the male gametes, though here not associated with any visible change in somatic cells because of the fact that the staminate inflorescence dies too soon after the pollen is shed? If male gametes do carry such modified factors and if the modification is as irregular in occurrence as the somatic modifications seen in variegated ears, so that any part of the tassel, from all to none, may produce gametes with the modified factor while not showing any visible somatic modification, it is obvious that the real nature of the male gametes of any variegated-eared maize plant can not be foretold. The mere fact that a variegated ear is self-pollinated, therefore, does not insure that its seeds are fertilized with pollen of known character.

That the male gametes of variegated-eared maize do often carry factors for self-red is shown by crosses of pure non-red strains with pollen from plants with variegated ears. The plants that furnished the pollen for these crosses were in some cases the same ones whose self-pollinated ears were concerned in the records discussed above. The results of these crosses are summarized here. Eight non-red ears crossed by plants that were homozygous for pericarp color yielded 17 red-eared, 116 variegated-eared and 8 white-eared⁸ plants. Similarly, 14 ears of pure non-red strains crossed by pollen from plants heterozygous for pericarp color yielded 26 red-eared, 192 variegated-eared and 229 white-eared plants. Considering merely the plants with colored ears, 22 crossed ears produced 43 red-eared to 308 variegated-eared plants, or a little over 12 per cent. self-red.

Since the male gametes of variegated-eared corn have now been shown occasionally to carry a factor for self-red, it is obvious that only from crosses of variegated-eared plants with pollen from pure non-colored strains, can a definite idea of the inheritance of the somatic variations in pericarp color be gained.⁹ Twelve ears from homozygous, variegated plants cross-pollinated by non-red strains might have afforded important evidence, but for the fact that 7 of them contained only narrow-striped grains and the other 5 no fully or even nearly self-red grains. The results are summarized here:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears.
More than one half red	5	11	0
Less than one half red	0	15	0
Narrow red stripes	2	281	0
Non-red	0	22	0

⁸ Some of the 8 white ears may have been extreme light types of variegation, for in some other cases very light variegated and wholly white ears have been observed on the same plant. And of course some of them may have been due to accidental pollination of the parent ear.

⁹ Though the genetic factors for pigment patterns in maize seem to be distinct from the factors for the pigment concerned in these patterns, no non-colored maize that I have used has ever given any indication in crosses of carrying pattern factors.

The principal facts of interest here are the production of only one red-eared plant to about 140 variegated-eared ones from narrow-striped seeds, and of about one red-eared to two variegated-eared plants from seeds with from one half to perhaps three fourths red.

Of 20 variegated ears, heterozygous for pericarp color, that were crossed with pollen from pure non-colored strains, 5 had only narrow-striped grains and 15 had variously broad-striped grains and even some self-red ones. The summaries of these crosses are as follows:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears
Self-red.....	9	0	11
Nearly self-red.....	5	0	2
More than one half red.....	4	2	2
Less than one half red.....	3	5	9
Narrow red stripes.....	7	265	301
Non-red.....	0	27	20

Here again, just as with homozygous, variegated ears, *the more red there is in the pericarp the more likely are the female gametes to carry a factor for self-red*. While the number of individuals dealt with are too few to afford reliable evidence, it is suggestive to note that the ratio of red-eared to variegated-eared plants, though not the ratio of red-eared to total plants, is greater in case of parent ears that are heterozygous than of those that are homozygous for variegated pericarp.

So far nothing has been said of the results in generations later than the one grown from the selected seeds (F_1). Let us now see what results follow when the variegated ears and the red ears produced as explained above become the parents of second generations (F_2) from the selected seeds. The variegated ears so produced behave like the original variegated ears from which seeds were selected and their progenies have, therefore, been included in the data already presented. There remains only to present the records of the progenies of red ears.

Data are available from 7 F_1 red ears obtained from self-pollinated, homozygous, variegated plants. Five of

these red ears were self-pollinated and two were crossed with pure white-eared plants. The results in F_2 and F_3 were as follows:

Seeds Planted from	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears
F_1 reds from selfed, homo., vgt'd. P_1 's			
5 ears selfed	119	37	0
2 ears \times white	46	45	0
F_2 reds from selfed F_1 reds			
1 ear selfed	9	2	0
1 ear selfed	16	0	0
F_2 reds from F_1 reds \times white			
1 ear selfed	26	0	5
2 ears \times white	40	0	37

The above is approximately what would have been expected, had the F_1 red ears that arose from self-pollinated, homozygous, variegated-eared plants been produced by a cross between red-eared and variegated-eared races.

Of the F_1 reds arising from self-pollinated, heterozygous, variegated-eared plants, nine were selfed and two were crossed with whites. The results secured in F_2 and F_3 follow:

Seeds Planted from	Self-red Ears	Variegated Ears	Non-red Ears
F_1 reds from selfed, hetero., vgt'd. P_1 's			
3 ears selfed (a)	104	23	0
1 ear \times white	6	7	0
6 ears selfed	105	0	38
1 ear \times white	12	0	7
F_2 reds from selfed F_1 reds of (a)			
4 ears selfed	59	12	0
1 ear selfed	23	0	0

From the above it appears that the F_1 red ears, arising from self-pollinated, heterozygous, variegated-eared plants behave in some cases as if they were hybrids between red-eared and variegated-eared races and in other cases as if they were hybrids between red-eared and white-eared races.

Of the four possible sorts of red-eared "sports" from variegated-eared plants, two remain to be treated. Be-

cause of their similar behavior they will be considered together here. Of the F_1 red ears arising from homozygous, variegated-eared plants that had been crossed with white-eared races, three were self-pollinated and two crossed with whites. Of the F_1 red ears arising from heterozygous, variegated-eared plants that had been crossed with white-eared races, four were selfed. The results in F_2 and F_3 are:

Seeds Planted from	Self-red Ears	Variegated Ears	Non-red Ears
F_1 reds from vgt'd. P_1 's \times white			
P_1 's homozygous			
3 ears selfed	54	0	16
2 ears \times whites	34	0	43
P_1 's heterozygous			
4 ears selfed	102	0	47
F_2 reds from selfed F_1 reds			
3 ears selfed	32	0	10
1 ear selfed	43	0	0

So far as these results go they indicate that F_1 reds arising from crosses between both homozygous and heterozygous, variegated-eared plants and white-eared races behave as if they were hybrids between red-eared and white-eared races.

One homozygous, variegated-eared plant was cross-pollinated by a homozygous red race. From the variegated ear produced, self-red, nearly self-red, and narrow-striped seeds were planted. All resulted, of course, in red-eared F_1 plants, 16 in all. A self-pollinated F_1 red ear from a narrow-striped seed gave in F_2 24 red-eared and 11 variegated-eared plants—somewhat fewer reds than were to have been expected. An F_1 red ear from a nearly self-red grain, when cross-pollinated with non-red, yielded 9 reds and 11 variegated in F_2 . A third F_1 red-eared plant, this one from a self-red grain of the variegated parent ear, bred true red in F_2 . One ear of this F_1 plant was selfed and yielded 14 reds in F_2 , and another ear was cross-pollinated by non-red and yielded 29 reds.

There are various other somatic variations rather frequently seen in maize, but they are apparently not in-

herited. There are sometimes found variegated ears with a large patch of self-red cob but with little or no corresponding change in the color of the overlying grains. I have as yet no evidence that this somatic variation in cob color is inherited through the seeds of the self-red part of the cob. Such seeds apparently always produce ears with variegated grains and variegated cobs, just as do other seeds of the same parent ear. Of course variegated seeds from a self-red patch of cob occasionally give rise to a self-red ear, as discussed in detail in this paper, and such red ears always have self-red cobs, but this is also true of all self-red ears, whether or not they are produced by red or by variegated seeds and without respect to whether the part of the cob underlying these seeds is self-red, finely variegated, or entirely white.

Another form of somatic variation seen in ears of maize is the occurrence of patches of considerable size, the grains of which, though variegated, are much darker in color than the grains of the rest of the ear. Such patches of grains are often quite as strikingly distinct in appearance as patches of self-red grains, and are apparently even more likely to correspond exactly in outline with an underlying patch of self-red cob than are patches of self-red grains. Moreover, such dark, variegated grains often present a rather definite color pattern. The crowns are often made to appear almost solid red by the widening and convergence at the crown of narrow red stripes extending down toward the base of the grain particularly on the side opposite the germ. Another type of dark, variegated grains differs from the lighter, variegated grains of the same ear principally in the greater development of the somewhat washed-out red apparently underlying the dark red stripes of the variegation pattern proper. I have grown numerous progenies from dark and light variegated grains of the same ears, but as yet have no evidence that such somatic variations are inherited. Notwithstanding this, I have strains of maize breeding true to a very dark type of variegation, others to a medium

sort of variegation, and still others to exceedingly light types of variegation. There can be no doubt that some of these different types of variegation are inherited, but the mode of inheritance in crosses has not been fully worked out.

One other form of grain coloration that might be called an extremely dark type of variegation is to be noted. The grains are self-red throughout except for a nearly colorless crown formed by converging light stripes extending some way down the side of the grain opposite the germ, almost exactly the reverse of one of the types of dark variegation described above. Variegations of this sort behave in inheritance almost exactly like fully self-red grains, giving a large percentage of red-eared progeny. And these red ears are apparently always fully self-red, never showing the pattern of converging light lines seen in the parent seeds. Many such seeds have been included in the results recorded earlier in this paper where they were listed as "nearly self-red."

INTERPRETATION OF RESULTS

Any interpretation of the data presented here must take account of these facts: (1) that the more red there is in the pericarp the more frequently do red ears occur in the progeny, and (2) that such red ears behave just as if they were F_1 hybrids between red and variegated or red and white races. The development of red in the pericarp is evidently associated with and perhaps due to a modification of some Mendelian factor for pericarp color in the somatic cells. The zygotic formula of a plant homozygous for variegated pericarp may be designated as VV , and that of a plant heterozygous for variegated pericarp as $V-$. If in any somatic cell VV , from unknown causes, a V factor were transformed into a factor for self-color, S , that cell would then have the formula VS . Any pericarp cells descended from it would without further modification be red. If all the pericarp cells of a seed were thus descended, the seed would be self-red, just as it would

if the plant bearing it were a hybrid between pure red and variegated races. Moreover, one half of the gametes arising from such somatic cells would carry V and one half would carry S , just as if the plant were a hybrid of red and variegated types. Or, if both V factors were changed, the grains would be self-red as before, but all instead of half the gametes would carry S . If, however, the modification from VV to VS should occur very early in the life of the plant, or even of the embryo, all the ears of the plant might thereby become self-red, and one half of all the gametes both male and female might then carry S and the other half V as in the ordinary hybrid. Or the plant might then become a sectorial chimera with one variegated ear and one red ear, the gametes from the one side of the plant all carrying V . If the modification occur much later, say soon after the ear begins to form, there might then be merely a solid patch of red grains on an otherwise variegated ear. In this case only those gametes arising from these smaller masses of tissue would carry half S and half V . If, however, the modification occur after the grains begin to form, the latter might be perhaps three fourths red, or one half red, or merely have narrow stripes of red, depending upon the amount of pericarp directly descended from the modified cell. In this case it seems reasonable to assume that the larger the mass of modified tissue the greater the chance that the gametes concerned should carry S . Finally, if in certain grains the change never occurs, they should show no red and the gametes formed in connection with them should all carry V , none S .

Similarly, it may be assumed that in any cell of a heterozygous, variegated-eared plant, V —, the V factor may as before become an S factor. The effect on pericarp color would be exactly the same as in a homozygous, variegated plant, and, of the gametes arising from the modified tissue, one half would carry S as in the other case, but the other half, instead of carrying V , would carry no factor and would be represented by —.

If the interpretation suggested here is correct, it is to be expected that the more red there is in the pericarp of any seeds, *i. e.*, the larger the mass of tissue descended from the cell in which the change from V to S took place, the greater the chance that the female gametes concerned carried the factor S . With heterozygous, variegated-eared plants, V —, however, never more than half of the gametes concerned could carry S even in case of self-red grains, the other half of the gametes carrying no factor, —. Of the heterozygous, variegated ears the progenies of which have been reported here, some were selfed, some crossed with white, and some open-pollinated. From self-pollinated ears, self-red and nearly self-red seeds yielded 32 red-eared, 9 variegated-eared, and 14 non-red-eared plants, or practically 58 per cent. self-red. This excess of self-red ears may be due, in part at least, to the presence of the S factor in some of the male gametes concerned, but the numbers are too small to give very reliable indications. From similar ears that instead of being selfed were crossed with white, so that the results could not have been influenced by factors present in the male gametes, self-red and nearly self-red seeds produced 14 plants with red ears and 13 with non-red ears, or about 52 per cent. red. While these numbers are very small, the fact that no variegated ears were produced, but that every ear with any red color was self-red, is noteworthy. From the open-pollinated, heterozygous ears included in my cultures self-red seeds gave progenies consisting of 171 red-eared, 32 variegated-eared, and 102 non-red-eared plants, or about 56 per cent. red.

In case of homozygous, variegated-eared plants, VV , all the gametes associated with seeds that later become self-red could carry S only if both V factors of the somatic cells from which the gametes arise were changed to S factors. Because of the rarity of changes from V to S , unless both V factors are influenced alike by whatever causes the change, so that both change simultaneously to S factors, the chance is slight that more than one will ever change.

In the latter case only about 50 per cent. of the gametes associated with self-red grains of homozygous, variegated ears could be expected to carry *S*, just as in the case of heterozygous ears. None of the open-pollinated ears whose progenies I have grown were homozygous for variegated pericarp, and none of the homozygous ears that had been crossed with white contained any self red or nearly self-red seeds. The only data, therefore, that bear upon the point at issue are those obtained from self-pollinated, homozygous, variegated ears. The self-red and nearly self-red seeds of such ears produced 64 red-eared and only 25 variegated-eared plants, or about 72 per cent. self-red. This may mean that in some cases both *V* factors were changed to *S* factors, but the results may just as likely be due to the presence of *S* in an unusually large percentage of the male gametes concerned. The production of the 25 variegated-eared plants, however, is very good evidence that, in at least a very considerable number of cases, not more than one of the two *V* factors could have been changed to *S*.

If the change from *V* to *S* should happen to occur at such a time that the grain rudiments became sectorial chimeras consisting of say one half modified cells and one half unmodified ones, one half of the pericarp would be expected to show red color and the other half no color. It would be expected further that the chances of a particular gamete's arising from a modified or from an unmodified cell would be equal. If then one half of the gametes associated with these one-half-red grains arise from cells in which only one of the *V* factors has been changed to *S*, one fourth of the gametes should carry *S* and three fourths should carry *V*, or one fourth *S*, one fourth *V*, and one half —, depending upon whether the ears concerned are homozygous or heterozygous for variegated pericarp. Such grains from homozygous ears should, therefore, whether selfed or crossed by white, yield about one red ear to three variegated ones. Similarly, from heterozygous ears, grains with one half their pericarp red should

yield about one red to two variegated to one white if self-pollinated and one red to one variegated to two white if crossed by white. (This is on the assumption that no *S* factors are carried by the male gametes.) Let us assume that by lumping together all the seeds listed in the foregoing records as "more than one half red" and as "less than one half red" the whole lot would average about one half red, and compare the results with the expectation as noted above. From grains of these two classes from homozygous ears both selfed and crossed by white, there resulted 19 red-eared and 82 variegated-eared plants, or a ratio of about 1:4.3 instead of 1:3. From heterozygous ears self-pollinated grains of these two classes yielded 54 red-eared, 85 variegated-eared, and 52 white-eared plants, and similar grains crossed by white yielded 7 red-eared, 7 variegated-eared, and 20 white-eared plants, or ratios of 1.04:1.63:1 and 1:1:2.86 instead of 1:2:1 and 1:1:2, respectively. The observed ratios are certainly suggestive but must not be given undue importance, for there is no assurance that the seeds used really averaged one half red and no assurance that some of the male gametes in the case of the selfed seeds did not carry *S*.

We must now examine the results secured in generations later than F_1 , and note whether the hypothesis under consideration applies equally well to them.

It will be recalled that F_1 red-eared plants that arose from homozygous, variegated ears which had been self-pollinated (see page 99) yielded in F_2 only red-eared and variegated-eared progeny. On our assumption the formula of the parent variegated ears was VV , but the red grains of these ears were VS and the gametes associated with them therefore either V or S or all S . Female gametes carrying S would have produced red ears in F_1 whether the male gametes carried S or V , and female gametes with V could not have produced red ears except when the male gametes uniting with them carried S . The F_1 red-eared plants must therefore have been VS or SS , the former being expected much more frequently than the

latter, owing to the rarity of S in male gametes. Only 7 such red ears were tested and all yielded red and variegated ears in typical Mendelian ratios, showing that all of them were VS like any F_1 hybrid between red and variegated races. Of two F_2 reds from selfed F_1 's, one again yielded reds and variegates and one apparently bred true red. Three F_2 reds, from F_1 reds crossed by whites, yielded reds and whites only—typical Mendelian results throughout.

When F_1 red-eared plants arose from either homozygous or heterozygous, variegated ears that had been cross-pollinated by whites they yielded only red-eared and white-eared, never variegated-eared, offspring (see page 100), just as if they were F_1 ears of a cross of reds with whites. By hypothesis the parent variegated-eared plants were $V-$ and VV , and their red grains $S-$ and SV (or possibly SS). The gametes associated with such grains were therefore S and $-$, and S and V (or possibly all S). The male gametes from white races were all $-$. The F_1 plants were therefore $S-$, $V-$, and $--$, only those with $S-$ having red ears. The five red-eared F_1 plants that were tested produced in F_2 red-eared and white-eared plants in Mendelian ratios. Of the F_2 red-eared plants one bred true in F_3 and three again segregated into reds and whites.

When heterozygous, variegated, parent ears were self-pollinated, the F_1 red-eared plants behaved in some cases like hybrids of red with variegated races and in other cases like hybrids of red with white races (see page 99). Our assumption is that the variegated-eared parent plants were $V-$ and their red grains $S-$. The gametes associated with these red grains were of course S and $-$. The male gametes of the same plants were doubtless largely V and $-$, though a few were probably S . The F_1 plants must therefore have been $--$, $V-$, $S-$, SV or SS . Reds with SS would be expected only rarely, and of the 11 F_1 reds tested none had that formula, else they would have bred true in F_2 . Seven of the 11 F_1 reds evidently were

S—, for they yielded F_2 progenies consisting of reds and whites only. Four of the 11 were obviously *SV*, for they yielded F_2 's of reds and variegates only. Of the latter F_2 reds, one bred true in F_3 and four again segregated into reds and variegates.

From a self-red seed of a homozygous, variegated ear that had been cross-pollinated by a pure red race, an F_1 red-eared plant was produced and this plant bred true red in F_2 . From a nearly self-red seed of the same variegated, parent ear, an F_1 red was produced but yielded reds and variegates in F_2 just as did a similar F_1 ear from a seed with narrow red stripes (see page 100). The variegated parent ear was *VV* and the red and near-red grains probably *VS*. The gametes associated with these grains were *V* and *S*. The male gametes were all *S*. Therefore the F_2 reds were in part *VS* and in part *SS*.

By way of summary, it is recalled that, in all, 28 F_1 red-eared plants were tested by F_2 progenies. Only one of these bred true and that one came from a red grain of an ear that had been cross-pollinated by a pure red race. Disregarding the three F_2 red-eared plants thus produced and the 9 red ears produced from seeds of variegated ears that had been cross-pollinated by white races and that therefore could not have bred true, there remain 16 F_1 reds, none of which bred true in F_2 . Had these F_1 red-eared plants behaved as did the F_1 green-leaved plants produced by green branches of variegated-leaved parents in Correns's experiments, approximately 5 of the 16 should have bred true. It will be recalled that Correns found that such green branches always produced green-leaved and variegated-leaved plants in the ratio of 3:1, and that one of the three bred true and the other two again segregated, just as must have happened if the green branch had been a part of an F_1 hybrid of green with variegated instead of a part of a homozygous variegated plant.

The difference between *Zea* and *Mirabilis* is, however, not a fundamental one, but is due merely to the circum-

stance that *Mirabilis* has perfect flowers while *Zea* is monecious. In *Mirabilis* both male and female gametes of a green branch arise from somatic cells in which the V factor has changed to a G factor. If a change in only one V factor is responsible for the production of the green branch, the somatic cells of such a branch must all be VG and the results reported by Correns are the only ones to be expected. With *Zea mays*, however, all the grains of one ear of a variegated-eared plant might arise from cells having VS , so that half of the female gametes would carry S , while little or no corresponding change might take place in the staminate inflorescence and therefore no (or very few) male gametes would carry S . From such an ear of maize only about one half, instead of three fourths, of the F_1 plants should have red ears and none (or very few), instead of one third, of the F_1 plants should breed true.

The occasional green plants ("a" per cent.) arising from variegated branches in Correns's experiments with *Mirabilis* are more nearly comparable to F_1 red-eared maize plants than are the green plants arising from green branches. It is quite conceivable that on a variegated branch the male gametes might arise from cells that are VG , while the female gametes arise from cells that are VV , or the reverse, though this difference between male and female gametes would hardly be so common an occurrence as with maize where the staminate and pistillate inflorescences are situated so far apart. It is worthy of note in this connection that of the occasional green plants produced by selfed seed of variegated plants in Correns's experiments with *Mirabilis* (see diagram, Fig. 2), less than one third bred true and more than two thirds segregated into green and variegated. (Correns indicates this merely by the signs $<$ and $>$ in connection with 33 per cent. and 66 per cent. respectively, in his diagram, and gives no indication of how much less than 33 per cent. bred true or how much more than 66 per cent. segregated.)

De Vries's results with *Antirrhinum* yield readily to

the same analysis used with *Zea* and *Mirabilis*. Selfed seed from striped-flowered branches gave a small per cent.—from 2 to 10—of red-flowered plants. Only a few of the red-flowered plants were tested and these were found to yield 76 per cent. red to 24 per cent. striped. Selfed seed from red-flowered branches of striped-flowered plants yielded 71 per cent. red-flowered and 29 per cent. striped-flowered plants, approximating the 75 per cent. and 25 per cent. indicated by Correns's results with *Mirabilis*. None of these red-flowered plants bred true, but only one test, and that of only a few plants, was made. The results were 84 per cent. red-flowered and 16 per cent. striped-flowered plants. It seems quite likely that had de Vries tested more red-flowered plants he would have found some of them to breed true.

Correns's results with striped and red flowers of *Mirabilis* differed in one important respect from his results with variegated and green plants of the same species, as well as from the principal results with *Zea* reported here and from de Vries's results with striped-flowered and red-flowered forms of *Antirrhinum*. When red-flowered plants arose from striped-flowered varieties of *Mirabilis*, they behaved just as did the green plants that arose from variegated forms. But selfed seeds from wholly red-flowered branches of otherwise striped-flowered plants yielded little if any larger percentages of red-flowered plants than did selfed seeds from striped-flowered branches of the same plants. It would seem that in case of *Mirabilis* flowers, when the self pattern arises as a somatic variation from the variegated pattern there is no corresponding change in the Mendelian factors for these patterns. In case of seed-sports from variegated-flowered to red-flowered plants, however, the factors for variegation are affected just as in case of green plants arising from variegated ones and of red-eared maize plants arising from variegated-eared ones. The apparently non-inherited somatic variations of maize plants, noted briefly earlier in this paper, are possibly of the same nature as

the somatic variations in variegated flowers of *Mirabilis*. Some of these variations in maize are self-red cob patches on otherwise variegated cobs, and dark, variegated grains occurring in patches or scattered over light, variegated ears.

GENERAL CONSIDERATIONS

The experiments of de Vries, Correns, Hartley, and East and Hayes, as well as the records reported in this paper, all indicate that certain somatic variations are inherited in strictly Mendelian fashion. All these somatic variations consist in the appearance of self-colors on plants that are normally variegated in pattern. The fact that variegated plants occasionally throw both bud-sports and seed-sports with self-colors is not, in general, to be taken as an indication that the variegated plants in question are heterozygous. Such behavior seems to be inseparably associated with variegation. Correns has pointed out (*loc. cit.*) that variegated *Mirabilis* plants can not be considered mosaics of green and "chlorina" types due to heterozygosis, since they do not segregate into chlorina and green, but into variegated and green. The same reasoning applies to variegation in the color of maize ears. Variegated-eared plants do not throw reds and whites, but reds and variegates. The conclusion seems irresistible that self-color occurring as a somatic variation is due to the change of a Mendelian factor for variegation into a factor for self-color. If this be granted, the behavior of these variations in later generations is a mere matter of simple Mendelian inheritance.

From the title of his paper and the tone of his discussion, it is clear that Correns regards, as the most significant feature of these inherited somatic variations, the change from a homozygous to a heterozygous condition. He even refers to them as cases of "vegetativen Bastardierung" or "autohybridization." To me, however, the essential feature is the change of one Mendelian factor into another. The fact that this modification of genetic factors results in a change from homozygosis to heterozy-

gosis seems wholly incidental. It follows from the circumstance that usually only one of the two V factors of somatic cells is modified. My own data do not in fact show that the change always affects only one of the factors at a time. While the results prove that this is true in a part of the cases at least, the F_1 ratios suggest the possibility of both factors being modified in some cases.

It is of course utterly impossible at the present time to conceive of the cause or even of the nature of this change in factors from V to S . We can only conjecture at present as to whether the change may possibly be associated with changing metabolic processes in the maturing plant, or perhaps be connected in some way with changing external influences, or even be a quality inherent in the V factor itself. It is perhaps significant that in maize, at least, the change, whatever its cause, occurs very rarely early in the life of the plant and apparently becomes increasingly more frequent as the plant matures. Wholly red ears in variegated-eared plants are extremely rare; large patches of red grains are somewhat less rare; individual red grains occur on most variegated ears; red stripes on the individual grains are very frequent, in fact all but universal in some strains, though in other strains—very light variegated ones—there may be only a few striped grains on a whole ear, the others being wholly colorless. As a matter of fact, even the presence of an ear with red pericarp throughout on a variegated-eared plant may not be good evidence that the change in factors occurred before the ear began to form. If the change took place before the ear was laid down, it would seem that the cob should always be self-red, since the red-eared progeny of such modified grains of the variegated parent plant invariably have red cobs, and cob and pericarp colors are coupled absolutely in later generations. But red ears, or nearly red ears, with light variegated instead of red cobs, have been found to occur as somatic variations on variegated-eared plants. Such behavior suggests that sometimes the factor change may occur almost simul-

taneously in the rudiments of every grain so that the grains become self-red while the cob remains variegated. We might, of course, account for the appearance of self-colored grains on a variegated cob on the basis of separate factors for cob and pericarp color¹⁰ by the assumption that one of these factors may be modified while the other remains unchanged. But we should then have the no less difficult problem of accounting for the universal appearance of red cobs with F_1 red ears without respect to whether the parent grains stood on red or variegated cobs.¹¹

Forced to its logical limit, our conception of the V factor is that of a sort of temporary inhibitor, an inhibitor that sooner or later loses its power to inhibit color development, a power that once lost is ordinarily never regained. Of course it may be that there is present in variegated maize merely a dominant factor for self-color, S , that is temporarily inactive, but that sooner or later becomes permanently active. Even if this be true, S as an active factor and S as an inactive factor are certainly as distinct in inheritance as they are in development and therefore deserve to be designated separately. And since in one case there results self-color and in the other variegation, the factors may as well be called S and V as anything else. It is of course also conceivable that the S factor may repeatedly arise *de novo*, though this seems very unlikely.

Whatever our conception of the nature of the factors for variegation and for self-color in maize ears, these factors are certainly as distinct in inheritance as any two factors could well be. Moreover, there is abundant evidence, which can not be given here, that they are strictly allelomorphic, as indeed they must necessarily be if one arises by modification of the other—this on the assumption that the factors are definitely localized in certain

¹⁰ Evidence that there are distinct factors for cob and pericarp color was presented in a previous paper on coupling and allelomorphism in maize. Ann. Rpt. Nebr. Agr. Expt. Sta., 24: 59-90. 1911.

¹¹ This problem is discussed in another paper on the simultaneous modification of distinct Mendelian factors. AMER. NAT., 47: 633-636. 1913.

chromosomes. Furthermore, these factors are to be regarded as *pattern* factors. Though they must influence the development of the pigment in order to produce a pattern at all, they are now known to be distinct in inheritance from the factors for pigment—a fact that I have been able to show by use of a race of maize with a peculiar brown pericarp in addition to races with red pericarp.

SUMMARY

A somatic variation in maize is shown to be inherited in simple Mendelian fashion. The variation has to do with the development of a dark red pigment (or in one stock a brown pigment) in the pericarp of the grains, often associated with the development of an apparently similar pigment in the cob and husks.

Plants in which this pigment has a variegated pattern may show any amount of red pericarp, including wholly self-red ears, large or small patches of self-red grains, scattered self-red grains, grains with a single stripe of red covering from perhaps nine tenths to one tenth of the surface, grains with several prominent stripes and those with a single minute streak, ears with most of the grains prominently striped and ears that are non-colored except for a single partly colored grain, and probably also plants with wholly self-red and others with wholly colorless ears.

It is shown that the amount of pigment developed in the pericarp of variegated seeds bears a definite relation to the development of color in the progeny of such seeds. This relation is not such that seeds showing say nine tenths, one half, or one tenth red will produce or even tend to produce plants whose ears as a whole or whose individual grains are, respectively, nine tenths, one half, or one tenth red. Experimental results indicate rather that the more color in the pericarp of the seeds planted the more likely are they to produce plants with wholly self-red ears, and, correspondingly, the less likely to yield plants with variegated ears.

Self-red ears thus produced are shown to behave in in-

heritance just as if they were hybrids between self-red and variegated races or between self-red and non-red races, the behavior in any given case depending upon whether the parent variegated ears were homozygous or heterozygous for variegated pericarp and whether they were self-pollinated or crossed with white.

It is suggested that these results may be interpreted by the assumption that a genetic factor for variegation, V , is changed to a self-color factor, S , in a somatic cell. All pericarp cells directly descended from this modified cell will, it is assumed, develop color, and of the gametes arising from such modified cells one half will carry the S factor and one half the V factor if only one of the two V factors of the somatic cells is changed, or all such gametes will carry S if both V factors are changed.

The V factor is thought of as a sort of temporary, recessive inhibitor that sooner or later permanently loses its power to inhibit color development, becoming thereby an S factor. Or it may be that the dominant factor, S , is temporarily inactive, but sooner or later becomes permanently active. Again, the S factor may repeatedly arise *de novo*. The cause of any such change in factors is beyond intelligent discussion at present.

The results of Correns with *Mirabilis* and of de Vries with *Antirrhinum* are shown to be subject to the same analysis as that used to interpret the results secured with maize.