VARIEGATION IN PLANTAGO

S. IKENO

College of Agriculture, Imperial University, Tôkyô, Japan

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INTRODUCTION

Plantago major, one of the commonest weeds in Europe and America, grows also almost everywhere in Japan, the form growing here being considered by our systematists to be a sub-species "*asiatica*". There are also many garden races of this species known here, of which some are now being used in breeding experiments in our Botanical Garden. Among others there is a variegated race of which figure 1 represents an adult plant, and figure 2 a number of young seedlings. In this variety parts without chlorophyll are at first nearly white but gradually become pale yellow. The variegated plants reveal themselves generally very soon after germination, because the cotyledons are usually variegated, but sometimes the cotyledons are entirely green and then their real nature can be discerned only after the formation of the first, second, or even the third foliage leaf. The variegated plants seemed at first to breed entirely true to type by self-fertilization, but later it was discovered that a few green plants are rarely produced from them. These green plants will be considered in a later section (see page 413).

F_1 GENERATION

In 1912 I hybridized one of these variegated plants with a self-colored green one, reciprocally. All F_1 plants made in both reciprocal ways were self green.

In *Mirabilis Jalapa,* according to CORRENS (1909, p. 303), the hybrid between a variegated and a green race is somewhat paler green than the original green plant, the green color being not perfectly dominant over the variegated condition. In Plantago I was unable to detect

FIGURE 1.—An adult plant of variegated Plantago, seen from above. Natural size.

any appreciable difference between the pure green parent and the F_1 hybrids, in the intensity of their green color. HERIBERT-NILSSON (1912, p. 109), in his hybridization experiments with variegated and green plants in certain species of Oenothera, secured green hybrids, but on treatment of leaves of these hybrids by the well-known iodine method of SACHS he found that some parts of the leaves, being unable to produce an excess of carbohydrates, did not stain blue. He concluded rightly that in this case the variegation is *apparently* but not *really* a pure recessive character. I have made the same experiment on leaves of the F_1 hybrids of variegated and green Plantago. I plucked the leaves of normal green plants as well as of F_1 hybrids in the evening of a bright summer day and treated them by the iodine method. Both kinds of leaves were stained intensely black and uniformly throughout their whole extent.

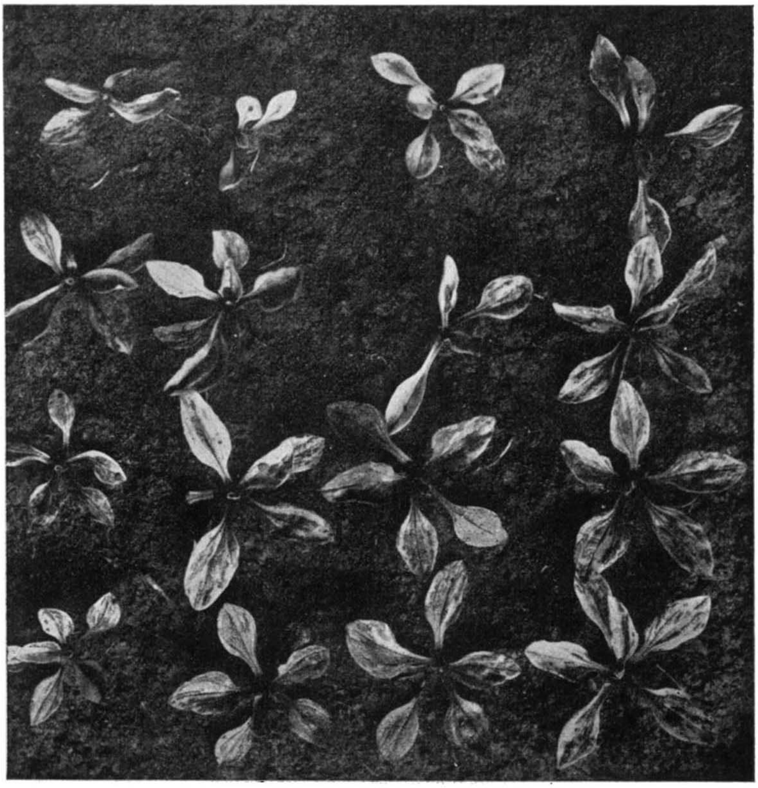

FIGURE 2.—Young seedlings of variegated Plantago, seen from above. Natural size.

Thus, neither in respect to the intensities of their green color nor concerning their mode of carbon assimilation is any difference to be detected between the green parent and the F_1 plants. We may conclude therefore that in Plantago the self-colored green is perfectly dominant over variegation.

F_2 GENERATION

The F_2 generation produced by the F_1 hybrids above described was found in 1913 to contain green and variegated plants in the ratios indicated in table 1.

TABLE 1

F_1 plant	F_2 generation			
	Number of green	Number of variegated	Totals	Ratio of green to variegated
Green × variegated	1176	82	1258	14.957 : 1.043
Variegated × green	1753	118	1871	14.991 : 1.009
Totals	2929	200	3129	14.977 : 1.023

From table 1 we have 2929 green and 200 variegated, both together 3129; or we have 14.977 green and 1.023 variegated per 16, thus $a = \pm 0.023$, while $E_M = \pm 0.047$.[1]

Thus we see that in F_2 the hybrids segregate in the ratio 15 green to 1 variegated, indicating that we are dealing here with a case of so-called polymery, which has become a well known phenomenon since the important discovery of NILSSON-EHLE (1909). When my experiments were begun there had been no detailed studies of the successive generations of such hybrids, except the work of NILSSON-EHLE, just cited, and that of EAST (1911). I decided therefore to study these Plantago hybrids in some detail. Meanwhile in 1914 appeared an elaborate paper by SHULL (1914 a) on the duplicate genes determining the capsule-form of *Capsella bursa-pastoris,* but I have continued my study, since not only is the character involved in my investigation entirely different from those previously studied, but also, as SHULL has pointed out, there are in the literature very few cases of polymery adequately proven.

It will be noticed here that for studying the later generations the hybrid green ♀ × variegated ♂ has been used exclusively, but there is no doubt that the reciprocal hybrid will behave in exactly the same way as the one actually used in the present experiments.

F_3 GENERATION

Before passing further I will consider briefly what results should be expected in the F_3 generation. If, for instance, we denote two factors or genes for the self-colored green plants by G and H, respectively, we have the formula $GGHH$ for green parents and $gghh$ for the variegated

[1] a = deviation from the expectation; E_M = probable error of the mean = $\frac{0.6745 \times \text{standard deviation}}{\sqrt{\text{number of individuals}}}$, i. e., $\frac{T\sigma}{\sqrt{n}}$

ones. In F_1 we have therefore $GgHh$ and consequently in F_2 we should have the zygotes represented by the following genetical formulae[2]:

Class 1	Class 2	Class 3	Class 4
$GGHH$ (1)	$GgHh$ (4)	$ggHh$ (2)	$gghh$ (1)
$GgHH$ (2)		$Gghh$ (2)	
$GGHh$ (2)			
$GGhh$ (1)			
$ggHH$ (1)			

The Arabic numerals in parentheses denote the number of individuals having the indicated genotypic constitution.

Of these 16 individuals, belonging to four classes, the one in class 4 is variegated and recognizable as such in F_2. I have already shown that the number of variegated plants actually secured in the F_2 approaches very nearly to this expectation (cf. table 1). The nature of plants belonging to the three other classes can be revealed only through their behavior in F_3. Each of the individuals of class 1 (7 in every 16) are expected to breed true to greenness in F_3, while those of class 2 and 3, each of them comprising 4 individuals in every 16, should yield green and variegated plants in the ratios of 15 : 1 and 3 : 1 respectively.

To ascertain whether this expectation is fulfilled 80 plants belonging to the F_2 generation were selected at random and grown to maturity. Seeds from each of these, produced by self-fertilization, were sown in 1914, and seedlings examined in 1914 and 1915. It was found that of these 80 plants, 37 produced exclusively green offspring.[3]

The number of seedlings arising from each of these parents was not specially counted, but generally several hundreds or sometimes even more than one thousand were raised from each. Of the remaining 43 F_2 plants, 25 were found to segregate in the ratio 15 green to 1 variegated, and 18 in the ratio 3 to 1, as shown in tables 2 and 3 respectively.

In table 2 we have thus 12855 green plants and 827 variegated, or 15.033 and 0.967 in 16; therefore we have $a = \pm 0.033$, while we have $E_M = \pm 0.022$, the deviation being 1.5 times the probable error of the mean.

[2] Only the designation of the genes and their number in each formula are here taken into consideration, but not their origin from the male or the female side respectively, it being taken for granted that both $GHgh$ and $ghGH$ are appropriately represented by $GgHh$.

[3] The pedigree Nos. of these 37 plants are: 3, 4, 5, 6, 9, 10, 17, 20, 21, 22, 28, 31, 32, 34, 40, 43, 46, 47, 49, 50, 53, 54, 55, 57, 59, 60, 61, 62, 63, 64, 66, 68, 78, 79, 82, 83, 86.

TABLE 2

Pedigree No. of F_2 plants	F_3 generation			
	Number of green	Number of variegated	Totals	Ratio of green to variegated
1	1448	80	1528	15.162 : 0.838
2	720	37	757	15.218 : 0.782
11	608	37	645	15.082 : 0.918
15	731	58	789	14.824 : 1.176
16	405	38	443	14.628 : 1.372
18	823	48	871	15.118 : 0.882
24	706	55	761	14.844 : 1.156
25	599	37	636	15.069 : 0.931
27	377	24	401	15.042 : 0.958
30	407	27	434	15.005 : 0.995
35	166	7	173	15.353 : 0.647
38	482	41	523	14.746 : 1.254
42	673	35	708	15.209 : 0.791
44	458	18	476	15.395 : 0.605
45	528	31	559	15.113 : 0.887
48	236	19	255	14.808 : 1.192
52	479	27	506	15.146 : 0.854
56	944	56	1000	15.104 : 0.896
72	119	14	133	14.316 : 1.684
73	52	6	58	14.345 : 1.655
74	99	12	111	14.270 : 1.730
76	260	15	275	15.127 : 0.873
80	655	55	710	14.761 : 1.239
81	639	41	680	15.034 : 0.966
85	241	9	250	15.424 : 0.576
Totals	12855	827	13682	15.033 : 0.967

In table 3 we have 6002 green and 1819 variegated plants, or 3.070 and 0.930 in 4; therefore we have $a = \pm 0.070$, while $E_M = \pm 0.013$. The deviation is thus a litte more than 5 times the probable error. This very small excess would not mean much, especially as the progenies fulfill the expectation very well in the next generation (cf. table 5 B, second part). The following fact may be noticed here, however. Our preliminary examination of variegated plants in 1912 and 1913 revealed the fact that their nature may generally be determined by the inspection of the cotyledons, which were at that time believed to be always variegated; so in 1914 and partly in 1915, seedlings were distinguished into green and variegated simply by the color of their cotyledons; tables 2 and 3 are the results of such countings. In the summer of 1915, however, it was discovered that sometimes, though not frequently, varie-

TABLE 3

Pedigree No. of F_2 plants	F_3 generation			
	Number of green	Number of variegated	Totals	Ratio of green to variegated
7	861	227	1088	3.165 : 0.835
8	627	210	837	2.996 : 1.004
12	613	189	802	3.057 : 0.943
13	700	214	914	3.063 : 0.937
14	329	121	450	2.925 : 1.075
19	241	111	352	2.739 : 1.261
23	425	90	515	3.301 : 0.699
26	311	120	431	2.886 : 1.114
33	467	134	601	3.108 : 0.892
39	201	42	243	3.309 : 0.691
41	153	39	192	3.187 : 0.813
58	130	37	167	3.114 : 0.886
65	178	50	228	3.123 : 0.877
67	53	12	65	3.262 : 0.738
69	10	6	16	2.500 : 1.500
70	25	10	35	2.857 : 1.143
71	312	98	410	3.044 : 0.956
77	366	109	475	3.082 : 0.918
Totals	6002	1819	7821	3.070 : 0.930

gated plants have green cotyledons, so that the true nature of such plants may be determined only after the development of the first, the second, or even the third foliage leaf. Since the summer of 1915 countings of green and variegated plants have not been made before the formation of their third leaf; tables 4, 5, and 8 are the results of such countings. The excess of the deviation over five times the probable error of the mean just above noticed is due to the insufficiency of the number of variegated plants, and this is in its turn due very probably to the fact that some variegated plants with green cotyledons were entered as green plants.

The 80 green F_2 plants selected at random were thus found to be composed of 37 individuals which breed true in F_3, 25 which segregated in the ratio 15 : 1, and 18 which segregated in the ratio 3 : 1. We have thus 37 : 25 : 18 or 6.94, 4.69, 3.37 in 15, against the expected ratio 7 : 4 : 4, the ratio of the respective numbers of these classes of F_2 individuals, as revealed by their behavior in F_3 generation, being well within the range allowed by the theory.

F_4 GENERATION

In the preceding paragraph I have merely described the mode of segregation of various classes of F_2 plants in the F_3 generation. In order to study the behavior of F_3 plants in the F_4 generation, we must first of all contemplate their genetical formulae, which are enumerated below, and compare with those of the F_2 plants from which each of them is derived, respectively. The variegated plants are enclosed in brackets.

	F_2	F_3
Class 1	*GGHH*	*GGHH*
	GgHH	*GGHH, GgHH, ggHH*
	GGHh	*GGHH, GGHh, GGhh*
	GGhh	*GGhh*
	ggHh	*ggHH*
Class 2	*GgHh*	*GGHH* (1), *GgHH* (2), *GGHh* (2) *GGhh* (1), *ggHH* (1), *GgHh* (4) *ggHh* (2), *Gghh* (2), [*gghh*] (1)
Class 3	*ggHh*	*ggHH* (1), *ggHh* (2), [*gghh*] (1)
	Gghh	*GGhh* (1), *Gghh* (2), [*gghh*] (1)
Class 4	[*gghh*]	[*gghh*]

If we look at the formulae of F_3 plants of various classes enumerated above, it will be easily seen that our expectation in F_4 should be as follows:

1. All individuals belonging to class 1, derived from green F_2 plants with no segregation of variegated plants, should again give green plants only;

2. Individuals belonging to class 2 should contain three kinds of green individuals: namely, those breeding true to greenness [*GGHH* (1), *GgHH* (2), *GGHh* (2), *GGhh* (1), *ggHH* (1)]; those segregating in the ratio 15 : 1 [*GgHh* (4)]; and those segregating in the ratio 3 : 1 [*ggHh* (2), *Gghh* (2)], the respective numbers of these three kinds of individuals being in the ratio 7 : 4 : 4;

3. Green individuals belonging to class 3 should be of two kinds, namely those which breed true to greenness [*ggHH* (1) and *GGhh* (1)], and those which segregate in the ratio 3 : 1 [*ggHh* (2) and *Gghh* (2)], the ratio of these two kinds of individuals being 1 : 2.

Let us see now whether or not this expectation is fulfilled.

For this purpose I have cultivated in 1915, 10 F_3 plants of class 1, 129 of class 2 and 68 of class 3, altogether seeds were secured from each of 207 of them by self-fertilization, and sown immediately after their collection. Unfortunately many of these seeds failed to germinate and no results whatever were obtained in this year, so that the examination of the segregation of the F_3 plants was postponed till 1916. In the latter year, however, many plants grown in 1915 had perished and only 108 plants remained with which to continue the experiment. These plants were:

1. Those of class 1. Only one or two F_3 plants derived from F_2 plants of each of the pedigree Nos. 3, 4, 5, 17, 46, 54, 55, 62, 63, 78,—17 in all (table 4);

2. Those of class 2. One to six F_3 plants derived from F_2 plants of each of the pedigree Nos. 11, 15, 25, 27, 35, 38, 44, 45, 48, 52, 72, 73, 74, 76,—65 in all (table 5 A);

3. Those of class 3. One to four F_3 plants derived from F_2 plants of each of the pedigree Nos. 7, 12, 13, 39, 58, 70, 71,—26 in all (table 5 B).

Plants arising from seeds of the above-mentioned 108 plants, by self-fertilization, were examined in 1916 and results are shown in tables 4, 5 and 6.

Table 4 represents the behavior of F_3 plants of class 1 and it will be seen that 11 of them produced green plants only.[4]

Green individuals belonging to class 2 may be distinguished as of three kinds, as we have expected, and these are shown in table 5 A. Of these three kinds those shown in the first part of this table breed true to greenness. In the second part are progenies aggregating 3428 green and 250 variegated plants, or 14.912 and 1.088 per 16; $\alpha = \pm 0.088$, while $E_M = 0.043$, the segregation in the ratio 15 : 1 being thus proven. The individuals shown in the third part of table 5 A yielded progenies consisting of 2763 green and 765 variegated plants or 3.133 and 0.867 per 4, i. e., $\alpha = \pm 0.133$, while $E_M = \pm 0.020$. Thus in the last case the deviation from expectation is more than six times the probable error. At the time the families entered in this table were grown, the seedlings were counted in a pretty advanced stage of their development, so that there should have been no such mistakes as were perhaps made in counting the seedlings in table 3, when it was not known that some variegated plants have green cotyledons (see p. 395); besides this deviation is much wider than in that case. This deviation is, as will be seen from the table, due to the insufficiency of the number of variegated plants and this latter fact may be probably explained by the weakness of variegated plants. From my long ex-

[4] The number of the F_3 progeny of this class was not counted, as noticed on p. 394.

perience in the cultivation of the variegated variety of Plantago, I have found that they, like variegated forms of other plant species, are of very weak constitution, this being due of course to their inadequate nutrition. Thus it was natural also to assume that the germination of their seeds is on the whole much poorer than that of normal green plants. To compare the rate of germination of seeds of both races sowings were made[5] and the number of seeds sown was compared with that of those which had germinated. The results are shown in tables 6 and 7. From these we see that even in the green plants the rate of germination is not very high (66.76 percent, table 6),[6] but in variegated plants it is much lower (45.41 percent, table 7). The insufficiency of the number of variegated plants above referred to, may in all probability be explained by this difference between the percentage germination of seeds of the two races. In table 7 it may be noted that in variegated plants the rate of germination is quite different in different individual spikes; thus in Nos. 9, 10 and 13 it is much higher than the average

TABLE 4

Pedigree No. of F_2 plants	Pedigree No. of F_3 plants	F_4 generation		
		Number of green	Number of variegated	Totals
3	1	266	0	266
	2	99	0	99
4	1	301	0	301
	2	412	0	412
5	1	213	0	213
	2	227	0	227
17	1	179	0	179
	2	433	0	433
46	1	274	0	274
	2	256	0	256
54	1	296	0	296
	2	210	0	210
55	1	185	0	185
62	1	280	0	280
	2	153	0	153
63	1	273	0	273
78	1	151	0	151
Totals		4208	0	4208

[5] Seeds were sown generally on the very day of their collection or sometimes on the day immediately following.

[6] As is well known the seeds of Plantago are very minute and consequently very poor in nutritive substances, which will perhaps account for their poor germination.

TABLE 5 A

Pedigree No. of F_2 plants	Pedigree No. of F_3 plants	F_4 generation			
		Number of green	Number of variegated	Totals	Ratio of green to variegated
11	1	136	0	136	
15	4	152	0	152	
	5	160	0	160	
25	2	141	0	141	
	3	435	0	435	
	6	489	0	489	
27	1	86	0	86	
	3	96	0	96	
	5	31	0	31	
	7	201	0	201	
	8	74	0	74	
	9	199	0	199	
38	1	59	0	59	
44	2	48	0	48	
	4	267	0	267	
	5	319	0	319	
45	1	399	0	399	
	3	104	0	104	
	4	409	0	409	
48	2	119	0	119	
	4	50	0	50	
	6	253	0	253	
52	2	301	0	301	
	4	346	0	346	
	7	247	0	247	
	8	200	0	200	
	10	338	0	338	
72	1	338	0	338	
	2	170	0	170	
	3	131	0	131	
74	1	249	0	249	
	4	286	0	286	
Totals		6833	0	6833	
15	3	86	5	91	15.121 : 0.879
25	4	111	6	117	15.179 : 0.821
	5	122	11	133	14.677 : 1.323
27	2	100	6	106	15.094 : 0.906
	4	128	13	141	14.525 : 1.475
	6	303	22	325	14.917 : 1.083
44	3	305	26	331	14.743 : 1.257
45	5	155	15	170	14.588 : 1.412
48	5	176	9	185	15.222 : 0.778

TABLE 5 A (continued)

Pedigree No. of F_2 plants	Pedigree No. of F_3 plants	F_4 generation			
		Number of green	Number of variegated	Totals	Ratio of green to variegated
52	1	162	14	176	14.727 : 1.273
	3	267	20	287	14.885 : 1.115
	6	183	12	195	15.015 : 0.985
	9	249	18	267	14.921 : 1.079
	11	334	24	358	14.927 : 1.073
72	4	195	16	211	14.787 : 1.213
73	1	40	3	43	14.884 : 1.116
74	3	449	28	477	15.061 : 0.939
76	1	63	2	65	15.508 : 0.492
Totals		3428	250	3678	14.912 : 1.088
11	3	264	76	340	3.106 : 0.894
	4	21	8	29	2.897 : 1.103
15	2	239	75	314	3.045 : 0.955
35	2	279	85	364	3.066 : 0.934
44	1	93	27	120	3.100 : 0.900
45	2	193	44	237	3.257 : 0.743
	7	380	99	479	3.173 : 0.827
48	1	122	31	153	3.190 : 0.810
	3	226	69	295	3.064 : 0.936
52	5	166	36	202	3.287 : 0.713
	12	135	25	160	3.375 : 0.625
72	5	146	34	180	3.244 : 0.756
73	2	84	21	105	3.200 : 0.800
74	2	95	26	121	3.140 : 0.860
	5	320	109	429	2.984 : 1.016
Totals		2763	765	3528	3.133 : 0.867

rate in green plants, (table 6), while in Nos. 5, 11, 14, 16, etc., it is very low and in No. 7 exceptionally poor. The insufficiency of the number of variegated plants in the third section of table 5 A may have been due to the fact that it included a large number of spikes containing seeds of variegated plants having poor germinating power. From all these considerations we may well conclude that in the families presented in the third section of table 5 A, the segregation took place in the ratio 3 : 1, though the deviation is somewhat greater than expected by the theory.

As will be seen from table 5 A there are three categories of green individuals of class 2; namely, those breeding true, those segregating

TABLE 5 B

Pedigree No. of F_2 plants	Pedigree No. of F_3 plants	F_4 generation: Number of green	Number of variegated	Totals	Ratio of green to variegated
7	4	144	0	144	
	5	58	0	58	
12	5	55	0	55	
39	3	203	0	203	
58	1	283	0	283	
70	1	222	0	222	
	3	128	0	128	
	4	209	0	209	
71	2	60	0	60	
Totals		1362	0	1362	
7	2	114	47	161	2.832 : 1.168
	3	132	47	179	2.950 : 1.050
	6	159	60	219	2.904 : 1.096
12	2	73	28	101	2.891 : 1.109
	3	279	98	377	2.960 : 1.040
	4	186	72	258	2.884 : 1.116
	6	108	34	142	3.042 : 0.958
13	1	224	63	287	3.122 : 0.878
	2	18	10	28	2.571 : 1.429
	3	162	43	205	3.161 : 0.839
	4	102	34	136	3.000 : 1.000
39	1	235	69	304	3.092 : 0.908
	2	188	78	266	2.827 : 1.173
	4	20	6	26	3.077 : 0.923
58	2	41	15	56	2.929 : 1.071
	3	66	24	90	2.933 : 1.067
71	1	152	47	199	3.055 : 0.945
Totals		2259	775	3034	2.978 : 1.022

in 15 : 1, and those segregating in 3 : 1, and these three categories are present in the respective numbers 32 : 18 : 15, or 7.39 : 4.15 : 3.46 in 15, which is very near to the theoretical expectation 7 : 4 : 4.

As to green individuals of class 3 we should have, as already stated on p. 397, two categories; namely, those breeding true and those repeating the segregation in the ratio 3 : 1, the number of individuals of these two categories being 1 : 2. In the first section of table 5 B are given those of the first category, all of which breed true. In the second part of the table we have a total of 2259 green and 775 variegated plants, or 2.978 and 1.022 respectively in 4; $\alpha = \pm 0.022$, while $E_M = \pm 0.021$,

TABLE 6

Green F_3 plants breeding true.

No. of spikes	Number of seeds sown	Number of seeds germinating	Rate of germination in percent
1	396	266	67.17
2	434	99	43.84
3	542	301	55.54
4	562	412	73.31
5	308	213	69.16
6	276	227	82.25
7	308	179	58.12
8	636	433	68.08
9	312	274	87.82
10	338	256	75.74
11	359	296	82.45
12	285	210	73.68
13	315	185	58.73
14	372	280	75.27
15	256	153	64.97
16	351	273	77.78
17	253	151	59.68
Totals	6303	4208	66.76

TABLE 7

Variegated plants.

No. of spikes	Number of seeds sown	Number of seeds germinating	Rate of germination in percent
1	316	149	47.15
2	251	103	41.04
3	168	96	57.14
4	279	120	43.01
5	277	92	33.21
6	110	71	64.54
7	148	14	0.96
8	198	126	63.64
9	90	67	74.44
10	132	103	78.03
11	159	60	37.74
12	202	88	43.56
13	71	64	90.14
14	249	62	24.90
15	305	148	48.52
16	353	137	38.81
Totals	3308	1502	45.41

expectation being thus pretty well fulfilled. Again, examination of table 5 B reveals the fact that there were 9 individuals breeding true (first section) and 17 segregating (second section), or 1.038 : 1.962, which almost perfectly fulfills the expectation above stated concerning the relative numbers of these two categories of individuals belonging to class 3.

Thus all results secured in F_4 progenies are pretty well in accordance with the theoretical expectation.

No further generations than F_4 were studied, but it is quite evident that F_5, F_6, etc., would give a repetition of the behavior here described for F_3 and F_4.

GENOTYPIC NATURE OF THE CONSTANT GREEN PLANTS

We have seen that there are some F_2 individuals which breed constantly green throughout successive generations, for instance Nos. 3, 4, 5, etc. Although all these green plants breed true by self-fertilization they are not all of the same genetical nature; or, in other words, they are *phenotypically,* but not necessarily *genotypically equal.* As shown on p. 397, individuals should be included in this group which have the genotypic formulae *GGHH, GgHH, GGHh, GGhh* and *ggHH.* To distinguish between these classes of genotypically different green plants it is necessary first to hybridize each of them with a variegated plant and to examine the progeny derived from the hybrids thus made. Then it will be easily seen that the hybrid *GGHH* × *gghh* will give green and variegated offspring in the ratio 15 : 1, *GGhh* × *gghh* and *ggHH* × *gghh* in 3 : 1, while in *GgHH* × *gghh* as well as *GGHh* × *gghh,* one-half will segregate in 15 : 1 and the other in 3 : 1.

To test the correctness of these assumptions, a number of constant green F_2 plants were selected at random and hybridized with a variegated plant, a large quantity of seeds being produced. Many of these failed to germinate, but fortunately I secured a number of hybrids sufficiently large for the purpose of the experiment. The constant green F_2 plants belonged to the pedigree Nos. 17, 54, 55, 62, 63, 64 and 78, and in 1915 I obtained from them 73 hybrids, all of which were self-colored green, the variegation being recessive. The self-fertilization of these hybrids in 1916 gave the results shown in table 8.

On examining the results shown in this table, the progenies of Nos. 17.I, 54.IX and 55.II, which are enclosed in brackets, should first be noted. The self-fertilization of these three plants gave not a single variegated offspring. As each of them was supposed to be a hybrid

TABLE 8

Pedigree No. of F_2 plants	Pedigree No. of F_2 green × variegated	Progeny of F_2 green × variegated: Number of green	Number of variegated	Totals	Ratio of green to variegated
	[I]	[55]	[0]	[55]	[1.000 : 0.000]
17	II	1084	71	1155	15.016 : 0.984
	III	93	36	129	2.884 : 1.116
	I	308	98	406	3.034 : 0.966
	II	162	40	202	3.208 : 0.792
	III	387	141	528	2.932 : 1.068
	IV	229	60	289	3.170 : 0.830
54	V	258	17	275	15.011 : 0.989
	VI	321	83	404	3.178 : 0.822
	VII	250	83	333	3.001 : 0.999
	VIII	13	6	19	2.737 : 1.263
	[IX]	[144]	[0]	[144]	[1.000 : 0.000]
	I	221	77	298	2.966 : 1.034
	[II]	[295]	[0]	[295]	[1.000 : 0.000]
	III	262	83	345	3.038 : 0.962
	IV	110	38	148	2.973 : 1.027
	V	124	42	166	2.988 : 1.012
	VI	119	52	171	2.784 : 1.216
55	VII	94	39	133	2.827 : 1.173
	VIII	106	35	141	3.007 : 0.993
	IX	32	12	44	2.909 : 1.091
	X	68	21	89	3.056 : 0.944
	XI	24	9	33	2.909 : 1.091
	XII	9	5	14	2.571 : 1.429
	XIII	26	18	44	2.364 : 1.636
	I	242	19	261	14.835 : 1.165
	II	456	27	483	15.106 : 0.894
	III	244	76	320	3.050 : 0.950
	IV	175	62	237	2.954 : 1.046
	V	471	44	515	14.633 : 1.367
	VI	194	61	255	3.043 : 0.957
	VII	117	34	151	3.099 : 0.901
	VIII	87	34	121	2.876 : 1.124
	IX	235	43	278	3.381 : 0.619
62	X	215	13	228	15.088 : 0.912
	XI	249	27	276	14.435 : 1.565
	XII	229	72	301	3.043 : 0.957
	XIII	163	14	177	14.734 : 1.266
	XIV	277	86	363	3.052 : 0.948
	XV	64	3	67	15.284 : 0.716
	XVI	186	14	200	14.880 : 1.120
	XVII	187	13	200	14.960 : 1.040
	XVIII	552	36[7]	588	15.020 : 0.980
	XIX	43	13	56	3.071 : 0.929

[7] Including two perfectly white seedlings which died soon after their germination.

TABLE 8 (continued)

Pedigree No. of F_2 plants	Pedigree No. of F_2 green × variegated	Progeny of F_2 green × variegated: Number of green	Number of variegated	Totals	Ratio of green to variegated
62	XX	161	25	186	3.462 : 0.538
	XXI	183	61	244	3.000 : 1.000
63	I	75	5	80	15.000 : 1.000
	II	302	21	323	14.960 : 1.040
	III	60	9	69	3.478 : 0.522
	IV	128	9	137	14.949 : 1.051
	V	136	13	149	14.604 : 1.396
	VI	49	3	52	15.077 : 0.923
	VII	42	2	44	15.273 : 0.727
	VIII	138	13	151	14.623 : 1.377
	IX	164	13	177	14.825 : 1.175
	X	108	12	120	14.400 : 1.600
64	I	361	27	388	14.887 : 1.113
	II	259	15	274	15.124 : 0.876
	III	263	24	287	14.662 : 1.338
	IV	175	9	184	15.217 : 0.783
	V	346	32	378	14.646 : 1.354
	VI	147	12	159	14.792 : 1.208
	VII	193	7	200	15.440 : 0.560
	VIII	199	26	225	14.151 : 1.849
	IX	49	4	53	14.792 : 1.208
	X	131	9	140	14.971 : 1.029
78	I	154	60	214	2.879 : 1.121
	II	108	49	157	2.752 : 1.248
	III	236	63	299	3.157 : 0.843
	IV	209	59	268	3.119 : 0.881
	V	322	120	442	2.914 : 1.086
	VI	54	27	81	2.667 : 1.333
	VII	69	17	86	3.209 : 0.791
	Totals	7392	554	7946	14.884 : 1.116
		6115	1949	8064	3.033 : 0.967

green × variegated, self-fertilization should have resulted in progenies consisting of both green and variegated plants. The fact that no variegated plants were produced must be accounted for. Two alternative explanations suggest themselves. On the one hand these cultures might be assumed to represent extreme cases of elimination of variegated plants through failure to germinate, owing to their constitutional weakness. It is indeed true, as already shown, that variegated plants are generally weaker in their bodily constitution than green ones, and also that the percentage germination of seeds is lower in the former than in the latter. In spite of these facts it is very improbable that no single variegated plant should have appeared if segregation really took place, because in 55.II, for instance, where 295 green plants appeared, more than 18 variegated plants should have been expected on the basis of the lowest available ratio, 15 : 1. Besides the progeny shown in the table, I have secured another consisting of more than 700 plants by saving seeds from two spikes of the same pedigree number, and yet no single variegated plant was secured. From these results I came to the conclusion that no segregation had here taken place and the first of the two alternative explanations was rejected. The second one, which is much more probable, and which I have adopted to account for the facts observed, is that these three families were from constant green plants which had slipped into the cultures through an error in technique, in spite of our utmost care to avoid such mistakes. This interpretation will not be considered at all improbable in view of the large extent of these Plantago cultures. The numbers of green plants in the progenies of these three plants are not counted in the totals, though they are included in the table for the sake of completeness, and are distinguished by enclosure in brackets.

A further point to be noted in table 8 concerns pedigree Nos. 62.XX and 63.III.

In the former the deviation (α) of the number of segregates for 4 or 16 is much larger than would be expected theoretically. According as this family is assumed to exhibit the 3 : 1 or 15 : 1 ratio, $\alpha = 0.462$ and $E_M = \pm 0.086$, or $\alpha = 1.151$ and $E_M = 0.192$, respectively, α being thus larger than $3E_M$ in either case. A definite determination as to whether this family exhibited the 3 : 1 or 15 : 1 segregation would be possible only by raising the progeny of later generations, but as all plants derived from this number perished long ago, the determination of this question is now impossible. The classification of this family, provisional as it was, was made in the following way: The quotient,

$$\frac{\text{deviation}}{\text{probable error of the mean}} = \frac{\alpha}{E_M},$$ when referred to the ratios 3 : 1 or 15 : 1, respectively, gives a measure of the relative closeness of fit of the observed results to either of these theoretical ratios. The family was classed under that ratio which gave the smaller quotient. This

quotient is $\frac{0.462}{0.086} = 5.372$ or $\frac{1.151}{0.192} = 5.995$, according as the family in question is considered to belong to the one or the other of these two classes, and as the former quotient is the smaller, this culture was put in the class 3 : 1. In No. 63.III the quotient $\frac{a}{E_M}$ is $\frac{0.478}{0.140} = 3.414$ or $\frac{1.087}{0.314} = 3.462$, respectively, and this family was put also in the class 3 : 1, in which the quotient is a trifle smaller.

Having disposed of these two doubtful families, let us now examine the general results as shown in table 8. If we sum up all the green plants derived from individuals whose progenies show segregation in the ratio 15 : 1, on the one hand, and all of the variegated plants of the same families, on the other hand, we have 7392 green and 554 variegated plants, or 14.884 to 1.116, respectively; thus $a = \pm 0.116$, while $E_M = \pm 0.029$. In the case of individuals considered to have segregated in 3 : 1 the corresponding calculation gives 6115 green and 1949 variegated plants, or 3.033 and 0.967, respectively; $a = \pm 0.033$, $E_M = \pm 0.013$. Thus although the deviations from expectation are not very small, yet they are not so large as to lie beyond the limits prescribed by theory.

Furthermore, from the examination of the table we see that there are three categories of F_2 individuals, namely,

1. Those which, being crossed by a variegated plant, give hybrids all of which segregate in 15 : 1. No. 64 belongs to this class.
2. Those of which all hybrids made by the same process, segregate in 3 : 1, to which class Nos. 55 and 78 belong.
3. Those of which hybrids made in similar way segregate partly in 15 : 1 and partly in 3 : 1, to which belong Nos. 17, 54, 62, and 63.

We may therefore represent No. 64 by *GGHH*, Nos. 55 and 78 by *GGhh* or *ggHH*, and Nos. 17, 54, 62, and 63 by *GGHh* or *GgHH*. Besides, as we have already seen on page 394, the number of constant green plants in the F_2 generation should be 7 in every 15, and of these 7, according to theoretical expectation, we should have the three classes just mentioned, in the ratio 1 : 2 : 4.[8]

[8] *GGHH* 1, *GGhh* 1, *ggHH* 1, *GgHH* 2, *GGHh* 2.

In table 8 we see that plants of these three classes, as revealed by experiment, occurred in the respective numbers of 1 : 2 : 4, which by chance exactly correspond to the theory.

Furthermore, *GGHh* × *gghh* and *GgHH* × *gghh* should each segregate either in 3 : 1 or 15 : 1, and individuals belonging to these two categories of segregation are expected to occur in *equal* numbers. Now if we examine table 8, we have in No. 17 only one individual from each class; this number is too small, however, for judging whether our expectation is fulfilled; in No. 62 we have 11 families showing 3 : 1 segregation and 10 which show a 15 : 1 ratio, a result which is as near as possible to expectation; while in Nos. 54 and 63 the numbers of plants exhibiting these two classes of segregation are very unequal. If the individuals of these four pedigrees are combined, the expectation is almost perfectly fulfilled, as shown in table 9.

TABLE 9

Pedigree No.	3:1	15:1
17	1	1
54	7	1
62	11	10
63	1	9
Totals	20	21

HAVE WE A CASE OF POLYMERY IN THE GREEN RACE OF PLANTAGO?

The production of a certain given character by the action of two or more independent factors or genes, each of which when separated from the other, is able to produce the same character, is a well known phenomenon, since the appearance of the important researches of NILSSON-EHLE (1909), and is called by different names by different authors. *"Polymery"* was first proposed by LANG (1911, p. 113) to designate this phenomenon. PLATE (1913, p. 155) introduced the word *"homomery"* instead of polymery. JOHANNSEN (1913, pp. 560-561) has distinguished two classes of polymery,—cumulative and non-cumulative. In the former case the action produced by two or more genes acting simultaneously is quantitatively larger than when but one is present, or in other words, the action of several genes accumulates; while in the latter class one single gene is able to perform a function both qualitatively and quantitatively equal to that produced by the conjoint action of several genes. JOHANNSEN reserves the name "homomery" for this latter class of polymery.

That several genes participate in the production of a given character is a very common phenomenon, but this does not necessarily represent a case of polymery, because in polymery two or more genes, each performs nearly the same function, while genes of very different functions may act together for the development of one character. For instance, according to BAUR (1910, p. 89) the green leaf color of Antirrhinum is due to three independent factors *Z, Y* and *N,* so that we have the formula *ZZYYNN* for the full green color. In this case three genes appear to act together to produce one character, but their respective functions were found to differ from each other, so that we have here no case of polymery. SHULL (1914 b) has shown a similar constitution with respect to chlorophyll factors in *Lychnis dioica* L. but in this case the factors *Y* and *N* seem to have more nearly like functions, the presence of either resulting in the production of chlorophyll, though not in equal amounts. Only in the presence of both *Y* and *N* are the plants dark green as in the wild species. To avoid the confusion between such a case and true polymery SHULL (1914 a, p. 120) has proposed the expressions "plural determiners" and "duplicate determiners." By "duplicate determiners" he means, "those which, when separated from each other, produce characters so like that they cannot be distinguished from one another", while by "plural determiners" he designates "those which independently produce a given character, or which modify it in any way whatever, which does not destroy its identity". Thus the duplicate determiners, which are a special case of plural determiners, correspond to polymery in the sense of LANG, while the plural determiners, not only include polymery, but also such cases as exemplified above in Antirrhinum, where several genes of different functions act conjointly for the production of one given character.

The question to be decided is whether or not the green race of Plantago here described represents a case of polymery. It has been demonstrated by the experiments here described, that the original green parent has the genetical formula *GGHH* in respect to its green color. When it is crossed with a variegated plant we have in F_2 as well as in later generations various zygotes containing either one or both genes *G* and *H,* as for instance *GGHH, GGhh, GgHh,* etc., yet all these are self-colored green like the original green parent. It is evident therefore that we have here a clear case of polymery.

We may further ask, whether or not any difference can be detected in the intensity of the green color according to the number of genes contained in each zygote, or in other words, is polymery in this case cumulative or non-cumulative in the sense of JOHANNSEN? Had we here a case of cumulative polymery we should find in F_2 and the succeeding generations plants of several gradations in respect to the intensities of their green color, because then we would have plants containing two kinds of genes in various combinations. During the earlier generations I paid no special attention to this question and there might have been possibly such slight differences which escaped my eyes. Observations and experiments were specially made in 1916 to detect such differences, if any existed. In that year I had in cultivation, a large number of F_2 plants of very different genetical constitutions; thus we had those represented by *GgHh* (segregating in 15 : 1 in F_3), others represented by *Gghh* or *ggHh* (segregating in 3 : 1 in F_3) and still others breeding true to greenness, which according to the results shown in table 8, are to be represented variously by *GGhh* (or *ggHH*), *GGHh* (or *GgHH*) and *GGHH*, thus we see that some zygotes contain only one kind of gene, others contain both, yet by careful comparison of these zygotes without the use of special colorimetric methods, I could not recognize any appreciable difference in the intensities of their green color. The following colorimetric experiment was then undertaken: From the leaves of nearly the same age on F_2 plants, Nos. 3, 4, 12, 17, 25, 46, 55, 62, 63, 78 (all constant green except 12 and 25), pieces of equal size (two from each leaf) were cut off by means of a cork-borer, according to the method adopted by CORRENS (1903, p. 140), and immersed separately in equal quantities of 90 percent alcohol in test-tubes of the same size. After a few days, alcoholic solutions of chlorophyll thus made were placed side by side to compare the intensities of their green color. Of the 10 individuals above enumerated, from each of which a chlorophyll solution was made, the genetical formulae of five were known, namely, Nos. 12 (*Gghh* or *ggHh*), 17 (*GGHh* or *GgHH*), 25 (*GgHh*), 55 and 78 (*GGhh* or *ggHH*). As to the remaining five zygotes, their exact genetical constitution is not known, but it might be expected that among these constant green plants were individuals which could be represented by *GGHH, GGHh, GgHH, GGhh, ggHH.* In spite of such diversities in their genetical constitution I was unable to detect any appreciable difference at all between the intensities of the green color of the chlorophyll solutions which were made from leaves of these several plants, by means of the method just described. A comparison by the colorimetric method was made between the green parent and the F_1 plants produced by crossing it with a variegated plant. The plants used in my original cross having perished long before the time when this experiment was undertaken, I simply transplanted into the garden a wild green plant growing in the place where the green parent of my original cross was collected, and hybridized it by a variegated plant. This new green plant had the same formula as the original green parent, i. e., *GGHH*, as revealed by the mode of segregation exhibited in F_2. Seeds from five spikes from as many different F_1 plants were sown and seedlings arising from them were counted separately, giving in F_2 the results shown in table 10. It is evident therefore that the F_1

TABLE 10

No. of spikes	No. of green	No. of variegated	Totals
1	50	4	54
2	150	7	157
3	26	1	27
4	63	6	69
5	30	2	32
Totals	319	20	339
or	15.056	0.944	16

$a = \pm 0.056$, $E_M = \pm 0.146$

plant has the formula *GgHh*. I made chlorophyll solutions from both plants in the way above indicated, compared them with each other as well as with each of the former series of chlorophyll solutions, but in this case also I was unable to detect any appreciable difference between the color intensities of these solutions.[9]

From the results of all these observations, either directly by eye without special aids, or by colorimetric methods, we have concluded that neither by the conjoint action of two or more genes of the same category nor by that of two or more genes of the different categories does any appreciable intensification of the color take place; thus only one gene is able to give rise to a reaction exactly equal to that produced by several genes acting together. In other words, we see here the complete dominance of genes, demonstrating that this is homomery or noncumulative polymery, in the sense of JOHANNSEN.[10]

[9] Chlorophyll solutions were also made from leaves of variegated plants and compared with those of green plants in the same manner as above indicated and it was quite evident that their green color is much less intense.

[10] It is not absolutely certain of course that had I employed much finer methods of colorimetric determination than were actually used, some differences of intensity of the green color might have been detected, but I may perhaps be allowed to say that if such differences exist they must be slight in the extreme and of no special importance.

COMPARISON WITH OTHER RACES

The hereditary behavior of certain variegated plants has been studied by some other authors. Variegated plants which follow Mendel's law when crossed with green plants, have always been found hitherto to segregate in F_2 in the ratio of approximately three green to one variegated (CORRENS 1909, BAUR 1910). Only in maize has EMERSON (1912, p. 94) found in some few cases ratios varying from 9 : 1 to 26 : 1 in F_2, and he thinks it possible that there are two factors involved, such that only in the absence of both is the plant variegated, but no further observations on this case have been reported. The variegated race of Plantago described in this paper is thus a new case, in so far as the presence of two duplicate factors has been duly proven, only in the absence of both of which is the plant variegated.

The fact that there are two or more factors for chlorophyll production has been discovered in some other cases, not by means of variegated plants as in our case, but by means of nearly pure white plants ("chloralbinos", SHULL 1914 b), or to borrow the expression of NILSSON-EHLE (1911, p. 18), by using the chloralbino instead of a variegated plant as an "analyzer." Thus, for instance, according to MILES (1915), in some varieties of maize the normal green plant has the formula *AABB;* plants represented by *aabb* and *AAbb* are pure white, while those represented by *aaBB* are yellowish-white, so that we have in this case two factors for green color, but since *AAbb* is different from *aaBB* we have here no polymery. In *Senecio vulgaris,* however, according to the investigations of TROW (1916) both *S. praecox* and *S. lanuginosus* are fully green, yet *praecox* × *lanuginosus* segregates in F_2 into 15 green to 1 white. It appears therefore that *praecox* and *lanuginosus,* both fully green, may be represented respectively by *AAbb* and *aaBB* and that among 15 green plants appearing in F_2, one fully green plant, represented by *AABB,* is found. Thus we have in the latter plant a case of polymery very similar to our green race of Plantago, though naturally it is unknown whether or not the factors *G* and *H* in Plantago are identical with *A* and *B* in Senecio.

THE PRODUCTION OF GREEN PLANTS FROM VARIEGATED

At the beginning of my culture experiments variegated plants seemed to breed perfectly true to type, but later it was discovered that a few fully green plants are produced from them even by self-fertilization. This fact is no new observation, however, because CORRENS (1909), BAUR (1910), and somewhat later, MILES (1915), have observed the same phenomenon in Mirabilis, Aquilegia and maize, respectively. According to the first of these three authors green plants thus arisen, either breed true or segregate into green and variegated in various proportions. In Plantago I have secured only a very few green plants of such origin; all of these have segregated into green and variegated, and I have found that the ratio of these two segregates has not been 15 : 1, as might be expected from the observations described above, but always approximately 3 : 1, as indicated in table 11.

TABLE 11

No. of spikes	No. of green	No. of variegated	Totals
1	110	37	247
2	39	15	54
3	60	21	81
Totals	209 2.965	73 1.035	282 4

$a = \pm 0.035$, $E_M = \pm 0.069$

No true-breeding green plants have yet been secured from variegated parents, but this may be due to the smallness of the number of green plants of such origin whose progeny I could examine. It seems not improbable that the cultivation of a much larger number of plants would yield such true-breeding plants as well as others which would segregate in the 15 : 1 ratio.

In the Mendelian hybrids thus far studied, green is always dominant over variegated, so that the production of green plants from variegated parents is a very remarkable phenomenon, whereby recessives give rise to dominants. In this connection it may be remarked that I could observe a very similar fact in another race of Plantago, concerning a character wholly different from the color.[11] From all my observations in respect to such phenomena I have been led to the view that in such cases we are dealing in all probability with the same category of phenomena, as that which is called "vegetative hybridization" (or "autohybridization") or a "recurring somatic variation", by CORRENS (1910) and EMERSON (1914),[12] respectively. My breeding experiments concerning this subject are under way and I hope to be able to publish the results of my investigations in a future paper.

[11] The breeding experiment of this race is now in its third year.

[12] EMERSON (1917) has recently changed the expression "somatic variation" to "sporophytic variation." [Note added in correcting the proof.]

SUMMARY

1. A variegated race of *Plantago major asiatica* was found to breed true to its type generally by self-fertilization, though sometimes it produced a few self-colored green plants by the same process.

2. The F_1 hybrids made between the variegated and the ordinary self-colored green plant, whether green $\times$ variegated or variegated $\times$ green, are in either case self-colored green, the latter condition being perfectly dominant over the variegation.

3. The self-colored green plant used as one of the parents in this experiment, was found to contain two factors, called G and H, respectively, such that the plant is variegated only in the absence of both of them. This fact has been fully demonstrated by the examination of the F_2, F_3 and F_4 progenies derived from the green $\times$ variegated F_1 hybrid.

4. Each of the two factors above mentioned, even when separated from each other, is able to produce the green color of exactly the same intensity as when both are present together. This is therefore a case of so-called *non-cumulative polymery* or *homomery* in the sense of JOHANNSEN, or the *duplication of factors* in the sense of SHULL.

5. The green F_2 plants which breed true to greenness in successive generations (constant green plants) are not always of the same genetical constitution and their respective genotypic nature has been revealed by hybridizing them with the variegated plants and examining the progenies derived from these hybrids, the F_1 hybrids from such crosses being necessarily self-colored green.

6. Each of the few green plants produced by self-fertilization of variegated plants (cf. 1 of this summary) was found to exhibit segregation in approximately the ratio 3 green to 1 variegated. Breeding experiments concerning this question are under way.

In conclusion, I may add that on account of their extreme minuteness the castration of flowers in Plantago is a very delicate operation which requires much patience as well as skill. I take much pleasure in thanking here two gentlemen, Mr. S. NOHARA and Mr. M. ANDÔ, for their kindness in executing this difficult task for me. I wish also to thank Dr. G. H. SHULL, editor of this journal, for revising this paper, as well as for his kindnesses in various other matters.

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