A genic survey of heritable characters in maize

I. Some new mutants

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(With 2 plates and 2 tables)

Introduction

Since 1937, an inbreeding of commercial varieties in maize has been carried out by T. SUTÔ, senior writer of the present paper, with the purpose of isolating inbred lines which have a highly combining ability of the hybrid vigor. One of the inbred lines, *T-41*, isolated from an old Japanese variety of flint corn, "*Kôshû-zairai*", which was collected from the "*Fuji-yoshida*", district situated at a table-land of Mt. Fuji, was found to be the best one in Hokkaidô as a parent of the cold hardy high-yield hybrid corn. This is the only one inbred line certificated by the Hokkaido Agricultural Experiment Station in the present status of corn breeding in Japan.

Up to date, about 50 new mutants have been found in the course of such inbreeding. Genetical research with those mutants was undertaken in an attempt to establish reliable evidence on the evolutional change of the heritable characters. Mutant genes may serve to throw some light on entirely new combinations of adaptive gene changes, even though they exhibit a retrogressive or deleterious change. More material and more data covering a wider range of mutant changes have therefore been gradually gathered as a further wrok additional to our inbreeding program. Some of the interesting findings obtained have at times been announced in both the annual meetings of the "Genetic Society of Japan" and of the "Botanical Society of Japan". Several such reports have already been presented as follows: (1) the genic analysis of monogenic mutants involving various variations in external morphology, pigmentation, chlorophyll character, chromosomal behavior and sex expression (SUTÔ, 1942, 1943, 1946, 1948 a, 1950, and SUTÔ & KATÔ, 1948), (2) the polymeric inheritance of a chlorophyll de-

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ficiency (SUTÔ, 1948a and 1949), (3) the cytoplasmic effect on the phenotypic expression of an old gold stripe controlled by a recessive gene, *og*" (SUTÔ, 1949 and 1950 a), (4) disturbed segregations due to the dominant gametophytic genes and the lethal genes (STUÔ, 1948 b and 1950 b), (5) the pseudo-allelic nature of some members of a *P*–allelic series (SUTÔ, 1951), (6) the specific nature of two dominant genes, P^{mo}, and *Tp*, affecting the character expression (SUTÔ, 1948 c and MATSUURA & SUTÔ, 1948), and others.

The present investigation was directed toward the gathering of information for the description of mutant characters and the linkage detection of mutant genes which are recognized to be inherited in the relatively regular manner of Mendelian segregation. A genic survey of nineteen new mutants described in the present report is presented with the sole object of recording and adding to our knowledge of the genetical nature of mutants.

Method of the linkage detection

In order to detect the linkage relation, the progeny test on hybrids of more than 500 combinations was made by artificially crossing of mutants with the ten linkage testers. Available data, by which the linkage relation of mutants was established, were obtained from the F_2 segregation in many cases and from the backcrossing segregation in a few cases. Linkage testers used, all of which were supplied by the late Prof. R. A. EMERSON of Cornell University to Prof. H. MATSUURA of our university in 1937, are the following: I) *br–f*$_1$*–bm*$_2$, II) *lg*$_1$*–gl*$_2$*–v*$_4$, III) *ts*$_4$*–lg*$_2$*–na*$_1$*–a*$_1$, IV) *su*$_1$*–la*, V) *bm*$_3$*–pr*$_1$*–v*$_2$, VI) *Pl-sm-py*, VII) *ra*$_1$*–gl*$_1$*–Tp–ij*, IIX) *ms*$_8$*–j*$_1$, IX) *c-sh-wx*, and X) *li*$_1$*–g*$_1$*–R*. Of those marker genes, six, *viz.*, *br*, *f*$_1$, *bm*$_2$, *na*$_1$, *v*$_4$ and *py*, were lost due to faulty cultivation, because the senior writer had to render service during two years, 1939 and 1940, with the Japanese colours. Thus, the "*P–E*$\widehat{\cdot}$*zl*" instead of the "*br–f*$_1$*–bm*$_2$" has since 1941 been used as a tester of the 1st linkage group, on the genetical ground that the locus of *P* and *E*$\widehat{\cdot}$*zl* on chromosome 1 is decided with certainty (SUTÔ 1951).

All of the data were treated statistically by MATHER's method of χ^2 to test the segregation ratio and the linkage relation. Firstly, an attempt was made to determine whether or not the observed segregation of giving genes is in accord with the hypothetical one expected from the Mendelian basis when judged by the calculated value of χ^2.

Mutants, showing the disturbed segregation which seems to be interpreted obviously by genetic mechanisms other than the simple Mendelian fashion, were excluded all from the present studies. Data arranged in Table 1 may therefore be stated to be all the simple monogenic inheritance concerning with the mutant character. A summary of the χ^2 analysis of genes involved in Table 1 is given in Table 2. The χ^2 values arranged in 4th and 5th columns of Table 2 were found in the majority of cases to agree with the expectancy from the simple Mendelian basis of segregation. There were also a few cases showing the significant value of χ^2, as can be seen in the segregation of genes such as *ij*, ad_5, ys_3, su_1, *Hs*, *cr* and *wt*. It was proved by data other than those in the present table that those clear-cut abnormal ratios of segregation are not so much due to a genic disturbance as to the following four external factors.

1). The viability of both ad_5- and ys_3- plants is definitely weaker than that of normal plants and often some of them die in the course of growth. The observed mutants are found always to have decreased in number, contrary to expectation, especially at the matured stage of plants.

2). The *ij* character has been well establisted by Rhoades (1943) to transmit mactroclinously from generation to generation. There is sometimes observed to occur a high variability of the segregation-ratio in the crossing progeny when the marker genes, *ij*, is used as the female parent.

3). Of the crossing kernels two types, sugary (*su*) and non sugary (*Su*), were chosen out and only a part of them was sowed separately in the segregation-testing field. The growing plants are not regarded as at random samples with respect to the sugary character of endosperm.

4). The phenotypic expression of the character controlled respectively by the four mutant genes, dm_2, Hs_2, *cr* and *wt*, is highly variable, ranging from nearly normal to extremely mutable phenotype. Thus, the classification of mutant character is too difficult to ascertain the actual rate of segregation concerned.

Accordingly, it is needful to revise the segregation data obtained with respect to those genes. In Tables 1 and 2, such revised number was denoted within parenthesis, by which values of χ^2 for both the segregation and the linkage were computed.

TABLE 1

Summary of linkage data

Genes X	Genes Y	Linkage Phase	*XY*	*Xy*	*xY*	*xy*	Total	Recombinations *p*(%)	Recombinations *sp*(%)	Linkage group
v_{21}	j_1	CS	140 150	41 27	32 21	23 23	236 221			
			290	*68*	*53*	*46*	*457*	*32.734*	*2.777*	IIX
$v_{.2}$	lg_1	RS	155 136	65 60	69 53	19 9	308 258			
			291	*125*	*122*	*28*	*566*	*41.199*	*3.447*	II
ys_3	ij	RS	264	93	64	2	423	*20.016*	*4.635*	VII
ys_3	ra_1	RS	217	85	111	10	423	*30.150*	*4.360*	VII
gs_3	lg_1	RS	270	85	82	21	458	*47.091*	*2.616*	II(?)
li_2	g_1	RS	138 129	49 36	45 34	12 8	244 207			
			267	*85*	*79*	*20*	*451*	*46.770*	*3.656*	X
ad_4	lg_1	RS	119	44	45	5	213	*33.489*	*5.996*	II
ad_5	v_2	RS	267	91	67	5	439	*29.558*	*4.342*	V
ad_5	bm_1	RS	274 (*129*)*	52	33	2	361 (*216*)	*34.273* (*25.267*)	*4.578* (*6.298*)	V
ad_6	g_1	CS	252	61	42	39	394	*32.313*	*2.962*	X
ad_7	d_{10}	CB	125	21	21	117	284	*14.789*	*2.100*	?
an_3	lg_1	RS	202	84	76	16	378	*40.455*	*4.247*	II
an_3	lg_1	CB	11 19	13 20	17 14	12 12	53 65			
			30	*33*	*31*	*24*	*118*	*54.237*	*4.586*	II
ma	ij	RS	184 107	54 34	85 49	12 2	335 192			
			291	*88*	*134*	*14*	*527*	*35.300*	*3.758*	VII
ma	gl_1	RS	182	76	96	10	364	*31.145*	*4.667*	VII
ma	la	RS	350 (*184*)	90	104	6	550 (*384*)	*29.851* (*22.735*)	*3.348* (*4.792*)	IV
ma	su_1	RS	357 (*191*)	93	97	3	550 (*384*)	*22.802* (*17.169*)	*4.003* (*4.921*)	IV
dm_2	bm_1	RS	409	108	48	11	576	*48.003*	*3.194*	V
Hs_2	cr	RS	65	103	59	59	296	*75.759*	*4.150*	?
Hs_2	wt	RS	74	138	40	54	306	*45.482*	*4.068*	?
cr	wt	CS	126	86	42	62	316	*39.451*	*3.699*	?

* The number in parentheses denotes the revised value calculated to be in accord with the ratio of 3 : 1 for the segregation of Y and y.

TABLE 2
Summary of the χ^2 analysis

Genes X	Genes Y	Linkage phase	χ^2_x	χ^2_y	χ^2_L	Kinds of χ^2
v_{21}	j_1	CS	*3.416*	*1.236*	*30.524* [2)]	Total
			2.714	*0.001*	*28.272* *	Deviation
			0.702	*1.229*	*2.252*	Heterogeneity
v_{22}	lg_1	RS	*2.108*	*1.393*	*8.492* *	Total
			0.681	*1.246*	*7.697* *	Deviation
			0.427	*0.147*	*0.795*	Heterogeneity
ys_3	ij	RS	*19.922* *	*1.457*	*9.383* *	
ys_3	ra_1	RS	*2.917*	*1.457*	*20.741* *	
gs_3	lg_1	RS	*1.540*	*0.841*	*0.428*	
li_2	g_1	RS	*2.799*	*1.548*	*0.633*	Total
			2.236	*0.710*	*0.499*	Deviation
			0.563	*0.838*	*0.134*	Heterogeneity
ad_4	lg_1	RS	*0.265*	*0.452*	*5.534* *	
ad_5	v_2	RS	*15.639* *	*1.640*	*6.698* *	
ad_5	bm_1	RS	*45.098* *	*19.414* *	*0.421*	
			[1)](*9.059*) *	(*0.000*)	(*5.198*) *	
ad_6	g_1	CS	*4.146* *	*0.030*	*24.376* *	
ad_7	d_{10}	CB	*0.225*	*0.225*	*140.845* *	
an_3	lg_1	RS	*0.088*	*0.004*	*5.278* *	
an_3	lg_1	CB	*3.072*	*0.185*	*1.063*	Total
			0.542	*0.136*	*0.847*	Deviation
			2.530	*0.049*	*0.216*	Heterogeneity
ma	ij	RS	*3.045*	*9.016* *	*14.080* *	Total
			2.672	*8.957* *	*13.072* *	Deviation
			0.373	*0.059*	*1.008*	Heterogeneity
ma	gl_1	RS	*3.297*	*0.366*	*18.173* *	
ma	la	RS	*7.333* *	*16.701* *	*6.533* *	
			(*2.722*)	(*0.000*)	(*34.241*)*	
ma	su_1	RS	*13.636* *	*16.701* *	*7.133* *	
			(*0.222*)	(*0.000*)	(*35.852*)*	

1) The numbers in parentheses have the same meaning as in Table 1.
2) * represents significant deviation from the expectation at a statistical level.
3) The results of the χ^2 analysis for the segregation of $dm_2 \cdot bm_1$, $Hs_2 \cdot cr$, $Hs_2 \cdot wt$ and $cr \cdot wt$ are neglected here (see text).

Nextly, a profitable approach to the linkage detection was also obtained by an analysis of χ^2, essentially similar to that appropriate to the segregation test of individual gene. A significant value of the linkage χ^2 implies itself a statistical meaning that the given two genes are not segregating independently of one another. In other words,

this is an evidence of the linkage relation. Actually, the χ^2 values of linkage are arranged in the 6th column of Table 2, of which most data are highly significant, showing the existence of linkage between the giving mutant and marker gene.

Description of mutant characters

1) *virescent seedling-21** (v_{21}^{a} and v_{21}^{β})**, IIX***

v_{21}^{a} was found in an inbred line (*S-119*) of a commercial variety "*Longfellow*" which was furnished by Hokkaidô Agricultural Experiment Station, and v_{21}^{β} in another one (*S-120*) of the same variety.

Both mutants are typical of the virescent seedling character. Young seedlings are yellowish in early stages, readily distinguished by color from the normal green seedlings. They rapidly turn color to green during the 6th or 7th leaf stage, but keeping the original yellowish color as many fine stripes on the normal green leaf-blade.

The phenotypic expression of virescence of the two mutants in relation to the temperature of the field during the seedling stages is very sensitive in the opposite direction to each other. That is to say, the v_{21}^{a} character is strongly influenced by the low temperature; v_{21}^{a}-seedlings become yellowish-white when grown in the cold temperature, much resembling the well-known *luteus* character (*l*) rather than the virescent. The chlorophyll is so deficient that seedlings sometimes tend to die before restoration to normal. The green color of the restored plant is however lighter than that of their normal sibs even in matured stage. The other seedling (v_{21}^{β}) is, on the other hand, influenced by the high temperature only; the virescent character can not be observed under the hot condition of the growing field, all seedlings showing normal appearance. The two mutants are therefore well distinguishable from each other by retaining the different phenotypes under the high temperature; v_{21}^{a} reveals a typical virescent character while v_{21}^{a} appears to become normal green.

The phenotype of F_1 hybrids between v_{21}^{a} and v_{21}^{β} is intermediate of both parents in virescent expression, being yellowish green in early seedling stages. However, no narrow yellow stripes are observable on the matured leaves, as can be seen in v_{21}^{a}. Furthermore, it is very interesting that there is a specificity in the F_1 hybrid nature as con-

* denoting the name of mutant character, ** gene symbol of mutant, and *** the name of linkage group inclusive of the given gene.

cerns the virescence. That is, (1) the virescent character seems to be markedly stable on the change of temperature, dissimilar to neither v_{21}^{α} nor v_{21}^{β}, and (2) in the F_2 segregation, the v_{21}^{β}-plants are a little more numerous than the v_{21}^{α}. A conclusion may be reached from those findings that the present two genes, v_{21}^{α} and v_{21}^{β}, should be considered to belong to a multiple allelic series; the genetic relation of v_{21}^{α} to v_{21}^{β} seems to be dominant on the temperature effect and to be recessive on the degree of restoration.

Of 457 F_2-plants, 236 are of the v_{21}^{α} hybrid and 221 of the v_{21}^{β} hybrid, which include the normal and virescent plants in the relation of 3:1, showing that there is a distinct monogenic segregation in the two in respect to virescent character. The gene, v_{21}, has its locus on chromosome 8 (Sutô, 1946), and a mean value of the recombination between v_{21} and j_1 was estimated to be ca. $33\pm3\%$ from the two coupling families, one of which came from a v_{21}^{α} hybrid and the other from a v_{21}^{β} hybrid.

2) *virescent seedling-22* (v_{22}^{α} and v_{22}^{β}), II.

Both mutants (v_{22}^{α} and v_{22}^{β}) came from inbred lines, *S-239* and *S-299* respectively, which were derived from a commercial flint variety, "*Onoa*" supplied by the "Yamato" Seed Co. Ltd.

Seedlings are pale green at first, but later gradually turn color to a beautiful yellow during stages from the 4th or 5th to the 10th leaf, and finally became more or less completely green. This nature is interesting in point of revealing the fairly yellowish color in the seedling stages later than in other virescent type. Mature plants are somewhat weaker than the normal ones, although the viability is good. The character is usually easy to classify under the favorable stages; v_{22}^{α}-seedlings are yellowish-white owing to complete lack of chlorophyll while v_{22}^{β}-seedlings are pale green yellow because they contain a small amount of chlorophyll. There is also a characteristic nature of phenotypic expression respecting temperature in that the former is stable to any change of temperature but the latter is strongly affected by temperature, revealing yellow color most strikingly in a cold year and, contrariwise, normal green in a warm year. The matured plants are green but a little lighter than those which are normal.

The F_2 plants showed a regularly monogenic segregation in almost exactly 3:1 ratio, actually numbering 220 green and 88 virescent in a v_{22}^{α} cross and 196 green and 62 virescent in a v_{22}^{β} cross, with a χ^2 of

1.393 and 1.246 respectively. The F_1 character in the cross between v_{22}^{α} and v_{22}^{β} is intermediate in color. But, the phenotypic expression on yellowing of color in F_1 plants is not so much affected by temperature as in v_{22}^{α}. Accordingly, v_{22}^{α} and v_{22}^{β} may be concluded to form a multiple allelic series of genes, and, if so, v_{22}^{β} must be dominant to v_{22}^{α} on the temperature effect, but incompletely recessive on other virescent nature. The locus of v_{22} is in chromosome 2 as indicated by the linkage data; v_{22} and lg_1 are loosely linked together with about $41\pm3\%$ of recombination in repulsion phase. Although v_4 has been well established to belong to the same linkage group, it can be easily distinguished from the present v_{22} by entirely lack of chlorophyll in the early seedling stage and by its revealing such lack of chlorophyll only in the lower part of the leaf blade, the tip of which is green having a trace of chlorophyll.

3) *yellow stripe-3* (ys_3), VII, Figs. 1 and 2.

This mutant was obtained from an inbred line (*S-288*) of a commercial variety of dent corn called "*Yellow Dent*".

Throughout all stages of the growing plant, it is very easy to make a distinction between the mutant and its normal sib according to the specific nature of chlorophyll deficiencies in the mutant. That is, (1) the mutant plant exhibits a pale yellowish-green color in the seedling stage, the same as in the typical virescent character, but (2) later develops green color rapidly along each of veinal ribs of the leaf blade in about the 4th or 5th leaf stage, so that all leaves of the matured plant are yellow in intervinal regions only but green in veinal regions, giving rise to a striped appearance which is composed of many longitudinal yellow and green bands alternately at regular intervals. Such a pattern is closely similar to the *yellow stripe-1* (ys_1) in the manner of striping, but the latter is fairly distinguishable from the former by showing the normal green seedling, the different linkage relation, and also by showing a high variability of the phenotypic expression instead of a higher degree of constancy as seen in ys_3. The mutant plants are usually weaker than their normal sibs. They are usually very slow to grow and often tend to die before reaching the maturity, and to bear a well-filled ear with great difficulty.

The *yellow stripe-3* is inherited as a recessive character, although the disturded segregations are sometimes found in crossing progenies owing to the bad viability. For example, a segregation comprising 357

normal and 66 ys_3 was observed in a case of F_2 families (Table 1), not corresponding with the expected ratio of 3:1 at all ($\chi^2 = 19.922$, see Table 2). It may be therefore certain that there is a decrease of ys_3 plants owing to the weakness in viability of the mutant. The linkage data obtained from the F_2 segregations in the repulsion phase indicates the locus of ys_3 to be on chromosome 7; a recombination value of ys_3 was calculated to be about 20±5% to *ij* and to be abut 30±4% to *ra*. Since the map distance between two marker genes used is well established to be 16 units (RHOADES, 1950), it may be concluded that their order is possibly arranged as "ra_1–*ij*–ys_3" on chromosome 7.

4) *green stripe*–3 (gs_3), II (?), Fig. 4.

This mutant was found in one (*S–318*) of the inbred lines which came from a dent variety, "*Yellow Dent*".

This character is similar to the yellow stripe mentioned above in type of the pattern, due to the presence of chlorophyll in all the veinal regions of the matured leaf-blade and the partial deficiency of chlorophyll in all the interveinal region. It is however very easy to draw a clear line between them; (1) seedlings are normal green instead of yellow, and (2) the interveinal space later turns to pale green instead of yellowish color, both owing to the chlorophyll defect. The classification holds good in the matured stages. The viability is very good, the same as in the normal plant. The degree of striping was found to be variable in its expression, grading from nearly normal to distinct striping. Chlorophyll-deficient areas of the striping leaf have usually a tendency to roll and to wilt under the bright sunlight condition of midsummer field.

gs_3 was reported by SUTÔ (1946) to be simple recessive to normal, and to be loosely linked to lg_1, which belongs to the 2nd linkage group, the recombination value being estimated at about 40%. There appears to be a liknage relation between them in the present case too, as well as in the previous case. Actually, a recombination value of approximately 47±3% can be estimated from a total of 458 plants in the repulsion phase of F_2 segregation. It may be demonstrated however from χ^2 analysis on the linkage relation that gs_3 and lg_1 should be independent genetically with characters inherited accrding to an expected ratio of 9:3:3:1 in the F_2 segregation, because a value of χ^2_L calculated as 0.428 is statistically not significant.

5) *lineate-2* (*li*$_2$), X, Fig. 2.

This was isolated from one (*S-104*) of the inbred lines obtained from a flint variety which has been known as "*Longfellow*" supplied by the Hokkaidô Agricultural Experiment Station.

The seedlings are very vigorous and grow rapidly, just like those of the normal type. When they reach the adult height, leaves begin to reveal this pattern of chlorophyll defect. The pattern is characterized by numerous small spots of very light color which are evident on the entire blade of matured leaves. They are arranged in a linear manner in the interveinal regions of leaf, especially remarkable in the midrib regions of the base of upper leaves. The present pattern is, as it were, a fine striping in the matured plants giving the leaf blade a grayish appearance on the whole. The phenotypic expression is widely variable, ranging from nearly normal in some crossing progenies to the distinct lineate type in the other ones, so that the classification is difficult in the former cases and good in the latter cases. The mutant plant has the same viability as the normal one.

Sutô (1946) reported already that the *lineate-2* is inherited as a simple recessive character and is loosely linked to g_1, giving a recombination value of about 48% in the repulsion phase of a F_2 segregation. An apparently similar finding was found in the present data, from which a recombination value can be calculated as about $47\pm4\%$, if it is estimated. Since a χ^2 for the linkage relation of *li*$_2$ to g_1 is not significant ($\chi^2_L = 0.633$), an actual deviation from the 50%-recombination, 3%, may be so negligible as to be non-significant. From the non-significancy of a heterogeneity-χ^2 (0.134) obtained, it may be further confirmed that both families used are to agree entirely in showing the presence of an independent segregation of 9 : 3 : 3 : 1 in the relation of *li*$_2$ to g_1.

This mutant (*li*$_2$) differs evidently from the *lineate-1* (*li*$_1$) in that the lineating character appears remarkably on the entire blade of matured leaves in the latter, rather than on the midrib region of leaf base as in the former, and also in that the latter has its gene-locus in the point of 15 units, left of the g_1 locus (Sutô, 1950 a).

6) *maculate* (*ma*), VII and IV, Figs. 2 and 7.

This mutant occurred in an inbred line, *S-251*, from a very early variety of flint corn, "*Kiwase*", furnished by the Hokkaidô Agricultrual Experiment Station.

It possesses a conspicuous pattern of chlorophyll deficiencies both in seedling and in matured stages, and can be well distinguished from the normal chlorophyll pattern by having, on the entire leaf, a great number of minute spots, all of which are yellow in color due to complete lack of chlorophyll. When seedlings first emerge from the ground they are green as seen in normal sibs. After 4 or 5 days, however, they lose their green color in a maculate manner, and later become pale yellowish green as it were a type of virescent seedlings. The minute spots are getting more and more clear cut in their features, appearing to scatter as a clearly yellow spotting of chlorophyll deficiency on the mature leaves. The phenotypic expression in the adult stage takes a great variation as to the number and distribution of spots either in the various plants of the same family or in the different leaves of the same plant. When spots are numerous they are arranged so closely as to form more or less continuous yellow areas in irregular lineate appearance. The growth rate is always slower than that of the normal plant in accordance with the density of spotting. In the extreme case, the viability is very weak, and hence, some of the mutants die, while the other mutants, whenever the spots are very a few in number, are practically like the normal plants in vigor. The classification is very good throughout all of the growing stages, especially remarkable in the seedlings.

According to a statement made by Sutô (1946), this mutant is due to a single recessive gene designated as *ma* which is involved in the 7th linkage group, with about 37% of recombination between *ma* and *ij* in the repulsion phase. It is very important to note that *ma* may be recognized with certainty from the present data not merely as belonging to the 7th linkage group as already reported by him, but also to the 4th linkage group. The recombination values of *ma* to the marker gener are as follows: $31\pm5\%$ to gl_1 and $35\pm4\%$ to *ij* in 7th linkage case while it is $23\pm5\%$ to *la* and $17\pm5\%$ to su_1 in 4th linkage case. A linear arrangement of those genes may be therefore given as "*ij–gl*$_1$*–ma*" and "*su*$_1$*–la–ma*" respectively. However, it will be necessary to make furthermore crossing experiments on a large scale before such a finding can be definitely stated to be true. If this be recognized as a fact, then there is another similar case, reported by Longley (1945). He concluded that the inheritance associated with genes, each of which is located on different chromosome, is to be termed as "*false linkage*" and results in the preferential segregation of chromo-

somes in his case. The present finding may be a case of such "*false linkage*" based on some unknown causes to be proved from the present data.

7) *yellow iojap striping* (ij^Y), VII, Figs. 2 and 16.

This has originated from a mutation of the marker gene, *ij*, in the course of inbreeding in our experimental field.

This pattern characteristically exhibits distinctly yellow stripes on both the leaf blade and leaf sheath instead of white stripes throughout all of the growing stages. The *yellow iojap* is inherited to be simple dominant to the *white iojap*, but recessive to normal green, both of which have been established to be of an allelic nature. The expression of those genes has been designated as ij^Y and ij^y respectively, both falling into the same locus on chromosome 7 (SUTÔ, 1946). Actually, the F_1 plant from a cross between the *white* and *yellow iojap* plants was of the same pure yellow stripe as the latter parent. An F_2 population involving a total of 96 plants segregated into 72 ij^Y, and 24 ij^y, this being in agreement with the expected 3 : 1 frequency ratio. The genetic behavior of ij^Y is entirely in accordance with that of the *withe iojap* (ij^y) except for the color difference of striping.

8) *yellow japonica–1* (j_1^Y), IIX.

The *yellow japonica* was discovered as a mutant of the gene marker stock (j_1) which is of the pure white striping nature appearing only in the matured stages. The genic relation of yellow to white of *japonica* stripe corresponds to the yellow to white relation in the *iojap* case as described above.

LINDSTROM (1918) found a similar striping of *japonica*, pure white in one type and pure yellow in the other. Such color difference was concluded by him to be due to an interaction with by another allele (*Ll*); the *whit japonica* is conditioned by a genotype of "*jjLL*" while the *yellow joponica* is by an "*jjll*". Those two kinds of *yellow japonica* found by Lindstrom and by the present writers are similar to each other in the phenotypic appearance, but differ evidently in the following heritable manners; (1) the present yellow is dominant to the *white japonica*, (2) the F_2 segregation on the present yellow and normal characters, as well as on white and normal ones, gives the 3 : 1 ratio of green to *yellow japonica*, as expected from the Mendelian monogenic basis, and (3) *white-japonica* plants were not observed at all in any progenies from the cross

between *yellow-japonica* and normal plants. Hence, the present white and yellow type of *japonica striping-1* (j_1) have been given by SUTÔ (1946) the gene symbols, j_1^w and j_1^y respectively, falling into an allelic series.

9) *sensitive japonica-1* (j_1^a), IIX, Fig. 15.

A *sensitive japonica* stock was isolated from one of the typical *japonica* stocks which have been known as the ornamental striped variety of rice corn called "*Nishiki-Morokoshi*", obtained from the Koishigawa Botanical Garden of the Tokyo University.

Its phenotypic expression, despite of the stable nature of its original *japonica*, is greatly influenced by environmental conditions in the cultivated field during the growing stages, especially by alterations in the temperature. If the temperature changes suddenly under unseasonable weather conditions, all of subsequently developing leaves fail to show any striping and turn essentially green, although some of them often contain a few fine stripes. For example, the plants when grown in the greenhouse, are regularly striped in the 5th or 6th leaf stages. But, whenever the halfgrown plants with distinct stripes are transplanted to the field, then there appears no striping on the later forming leaves probably owing to the temperature change (Fig. 15). The gene controlling such a *sensitive japonica* character was termed as j_1^a, considering it as a member of the *j*-allelic series. j_1^a is dominant over j_1 in the phenotypic effect by the temperature.

10) *adherent-4* (ad_4), II, Fig. 5.

This came from one of the inbred lines, *S-129*, which are of the "*Longfellow*" variety of yellow flint corn obtained from the Hokkaidô Agricultural Experiment Station.

The plants are normal in the seedling stages, but later all of their leaves adhere one another to various degrees in the various plants. In conspicuous cases, bracts and inflorescences in addition to leaves closely coalesce too. Accordingly, the upper leaves are often so firmly compacted that they are not separable, adhering into a mass which is frequently ruptured by the growth force of culm (Fig. 5). In an unconspicuous case, the adhered parts of the leaves are separated naturally with the growing pressure so that the plant becomes apparently normal in the matured stage. The classification is fairly easy in matured plant. The viability is as good as in normal plants.

This is inherited as a simple recessive character controlled by

a gene, ad_4. The segregation data indicate that ad_4 is linked to lg_1 with about 33±6% of recombination in the repulsion phase of F_2 segregation.

11) *adherent-5* (ad_5^a and ad_5^β), V, Fig. 11.

A type of adherences was found in an inbred line, *H-23*, isolated from the "*Yellow Dent*" variety which was furnished by the Hokkaidô Agricultural Experiment Station, and is characterized by the strongly inhibiting nature of adherence in seedlings (Fig. 11).

Adnerent-1 (KEMPTON 1920), *adnerent-3* (EYSTER 1934) and *adherent-5* are too much alike in their appearance in the seedling stage to distinguish. The mortality of seedlings is often high in extreme cases. However, the plants recover gradually to normal stature as they grow. After the ear bearing node developed, their adherent nature is manifested again. The degree of adherence is however so very little in the matured stages that some of the plants give themselves a normal appearance. The classification is very easy in seedlings but sometimes difficult in matured plants.

This mutant is conditioned by a recessive gene termed ad_5^a. A different type of adherences occurred in the pedigree cultures of ad_5^a-stocks, discriminating the latter from the former in the less adherence of seedlings; for the latter the gene symbol was designated as ad_5^β. The F_1 plants from a cross made between ad_5^a and ad_5^β are of the ad_5^β nature in phenotype, and their F_2 segregations were found to occur in a 3:1 ratio in a total of 83 plants, of which 56 are of ad_5^β-type and the remaining 27 of ad_5^a-type. Accordingly, ad_5^a and ad_5^β may be allelic and then the former should be recessive to the latter. The data concerned with the linkage relation was obtained from the two crosses in the repulsion phase of F_2 segregation as summarized in the present tables. One cross was made between ad_5^a and bm_1 and the other one between ad_5^β and v_2, and their recombinations were estimated as 25±6% and 30±4% in a total of 216 and 439 plants respectively. It may be therefore assumed that ad_5 is located on chromosome 5 and its linear sequence is given as "bm_1-ad_5-v_2", because the map distance between bm_1 and v_2 has been difinitely established to be 66 units (RHOADES, 1950).

12) *adherent-6* (ad_6), X.

This may have arisen through a mutation in one of the 10th linkage testers, "*Og-li-g*", supplied by the late Prof. EMERSON of Cornell University, U.S. of A.

The adherent nature can be seen in the matured leaves only, especially remarkable in the top regions of the leaves. The phenotypic expression is of a considerably low degree as compared with that of the other adherent characters. There occurs little adherence excepting in the upper matured leaves. The classification is frequently difficult even in the matured stages. The viability is very good, just like a normal plant.

This is a simple Mendelian character, recessive to the normal one. Its linkage data gives ad_6 to fall under the 10th linkage group. An F_2 segregation of a total of 394 plants in the coupling phase may lead to a conclusion that there is probably a recombination value of about $32 \pm 3\%$ between ad_6 and g_1.

13) *adherent-7* (ad_7), chromosome unknown. Fig. 8.

This was found in our cultures in which the "*Kiwase*" variety of early flint corn obtained from the Hokkaidô Agricultural Experiment Station is grown.

Seedlings are normal. The adherence develops rapidly in the 5th or 6th leaf stages. All the leaves, bracts and inflorescences are adherent to one another to a high degree in later stages. The adherent expression seems to be the most remarkable amongest all the heritable adherences. Frequently, the adherence is so firmily compacted as to prevent further growth, resulting in the highly abnormal stature of the plant. Owing to such growth inhibition by adherence, culms as well as ears are often forced into a contortion, and tassels are also compressed into a solid mass never expanding into the proper panicle. Accordingly, plants are unable to bring forth kernels unless artificial pollination is done. The present adherence resembles ad_1 and ad_4 in some case of phenotypic expressions, but differs from them in the strongly adherent nature and in its stable appearance.

This adherence is associated with a dwarf character which has been denominated by the writers as "*dwarf-10* (d_{10})" as seen in Fig. 6. Such two different characters are proved to be so closely linked together that they have been rarely segregated in descendants. Each of them was a monogenic character showing the recessive inheritance in the simple Mendelian basis. They are calculated to recombine in frequency of about $15 \pm 2\%$ in the coupling phase of a back-crossed population containing 284 plants. However, there is no data at all to decide whether their loci are on any of chromosomes.

14) *anther ear-3* (an_3), II, Figs. 3, 9, 10, and 17.

The two mutants by the same gene termed as an_3 were found independently in two different inbred lines, of which one, *S-152*, was isolated from the *"Sapporo-Hachigyô"* variety of early flint corn and the other one, *S-296*, from the *"Yellow Dent"* variety of medium dent corn. Botn varieties were supplied by the Hokkaidô Agricultural Experiment Station.

The character appears in all growing stages, being especially conspicuous in the matured stages. Leaves are characteristically short, broad and thick in comparison to normal, in seedlings (Fig. 10) as well as in matured plants (Fig. 3). Culms of matured plants are ordinarily shorter than normal ones, due to the shortness of internodes, resulting in the semi-dwarf stature. There is however a marked variability in height expression among different plants, ranging from the dwarf-like stature of less than one-fourth the height of normal culm to the nearly normal stature. Such difference in height is apparent even in seedlings although it is never so remakable as in matured plants. The tassel appears to be normal but sheds little or no pollen due apparently to failure of the glumes to open normally. Pollen grains collected artificially from anthers are always functional. The plants develop stamens well throughout the ear, especially in its upper parts. The upper end of the ear changes therefore into an unbranched spike-like structure which is composed of staminate flowers only. Kernels usually develop in the basal parts of ear. The classification is often possible in seedling stage and very easy in later stages. The viability is very good, much the same as that of normal plants.

It was already demonstrated by Sutô (1946) from F_2 repulsion data that this mutant is inherited as a simple recessive character and hence the gene determining it is to be termed as *"an_3"*; also it may have its locus in chromosome 2. The existence of such a linkage relation between an_3 and lg_1 may be further supported by the present data of the same F_2 segregation. Then, χ^2_L was 5.278 and a recombination value can be calculated as about $40 \pm 4\%$, this corresponding with a previous value estimated as 44%. But, there is not any evidence from the two backcrossed data of the coupling phase (Table 1) to support such a linkage relation because χ^2_L is 1.063 and its heterogeneity χ^2 is 0.216. If an estimation has to be made, a recombination value is computed as about $54 \pm 5\%$, making it meaningless statistically. In order to ascertain the

linkage relation of an_3, it will therefore be necessary to perform further experiments.

15) *dead leaf margins-2* (dm_2), V, Fig. 12.

This mutant was isolated from an inbred line, *S-201*, of the late flint "*Daichô-ou*" variety which has originated in northern China, supplied by the Hokkaidô Agricultural Experiment Station.

The character is expressed in the margins of upper leaves as the plant matures. The leaf margins of matured plants are dead and ruptured in the typical cases. The dead bands appear often on the interveinal regions of matured leaves in the extreme cases, varying in number from nothing (resulting in normal appearance) to several (similar to the green striping) per leaf. The vigour is the same as in normal plants. The classification is fair in matured leaves only, but impossible in seedlings and in growing leaves before the flowering time.

This is a Mendelian recessive character controlled by the single gene called "dm_2", and may be very loosely linked to bm_1 judging from a χ^2_L test of an F_2 segregation in the repulsion phase. The percentage of their recombinations was calculated as about $48 \pm 3\%$. Such a value is however within the fiducial limit of 5% level of probability for the expected value, 50%, fitting a hypothesis of independence, so that it may be premature to conclude the presence of such a linkage relation from the present data.

16) *Hairy sheath-2* (Hs_2), Figs. 13 and 14, chromosome unknown.

17) *crinkly leaf-4* (cr_4), chromosome unknown.

18) *wheat tassel* (*wt*), Fig. 13, chromosome unknown.

A mutant plant was found in our corn field wherein the "*Shirohazekibi*" variety was cultivated, furnisded by the Hokkaidô Agricultural Experiment Station. It expressed the following three specific characteristics in the mature stage only.

a). The pubescence on the sheath-surface of upper leaves is very remarkable for density and also for length of hair as compared with the normal pubescence.

b). The upper leaves are always so conspicuously crinkled that they are often rolled up, but not adherent together so as to be said to show adherence.

c). The tassel consists of an unbranched panicle resembling the wheat-panicle in appearance, although its size is larger than the latter.

Those characters were named as *Hairy sheath–2*, *crinkly leaf–4* and *wheat tassel* respectively, and each of the corresponding genes respectively was designated as Hs_2, cr_4, and *wt* (Sutô, 1946). When this mutant was crossed with normal plant, the F_1 plant is always hairy but less than the mutant parent in density of hairiness. All of those three characters appear in F_2 plants, *Hairy sheath–2* as dominant and the other two as recessive. However, their phenotypic expressions are extremely variable in every character, so that it is sometimes difficult to separate mutant plants from normal ones in the F_2 population, showing no clear cut segregation. In the present data, the number falling under each of the classes may be rather uncertain. Thus, the results of χ^2 tests are not arranged in the present table. But, it may be clear from the present F_2 segregations that those three are linked together and have their loci at least neither in chromosome 2 nor in 5.

According to reviews by Eyster (1934) and by Emerson et al (1935), Hs_2 is similar to Hs_1 in general appearance but differs in pubescent nature, in regard to which Hs_2 has a tendency of producing hairs in the vertical direction to culm (Fig. 14). *crinkly leaf–4* is also like to the other crinkled characters (e.g., to cr_1 and cr_2), but distinguished from the latter two by the fact that the crinkly character is never recognizable in seedlings at all.

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Summary

A genic study of nineteen mutants of maize, of which eighteen are

inherited to be recessive and only one (Hs_2) to be dominant, is reported and their characteristics were compared with their normal sibs. From the linkage relations of these mutants to marker genes, it was established that the mutant genes are located on the chromosome as follows: v_{22}, gs_3 (?), ad_4, and an_3 on chromosomes 2; *ma* on chromosomes 4 and 7; ad_5 and dm_2 on chromosome 5; ys_3 and ij^Y on chromosome 7; v_{21}, j_1^Y and j_1^a on chromosome 8; li_2 and ad_6 on chromosome 10. Further, of the remaining five, two, ad_2 and d_{10}, and three, cr_4, Hs_2 and *wt*, are linked together independently to one another but their loci on the chromosomes are not yet known.

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P.S. The present study was started, under Prof. H. Matsuura's project, by Dr. T. Akemine of our university in 1935. T. Sutô, senior writer, has been doing it since 1937, and cooperated since 1946 with two junior writers, Y. Katô and N. Mukaigawa. In the present study, field experiments were carried out by all of writers, and both the calculations of χ^2 and of recombination values mainly by Mukaigawa. The manuscript was completed by the cooperation of Katô and Mukaigawa, and translated into English by Sutô.

Explanation of Plate

Plate XII

Fig. 1. A *yellow striping-3* leaf.
Fig. 2. Some patterns of chlorophyll deficient characters on leaves; from the left to right, 1st: *yellow striping-3*, 2nd: *lineate-2*, 3rd: *yellow iojap striping*, 4th and 5th: normal, 6th: *maculate*, and last two: *blotched leaves* governed by a polymeric series of genes (bl_3, bl_4, bl_5, bl_6 and bl_7).
Fig. 3. A semi-dwarf type of *anther ear-3* plants.
Fig. 4. An adult plant having *green striped* leaves (gs_3) linked with *liguleless-1* (lg_1) (the right one); the left one is its normal sib.
Fig. 5. The right shows upper part of *adherent-4* plant and the left of the normal plant.
Fig. 6. *dwarf-10* plants.
Fig. 7. The sectioned part of a *maculate* leaf.
Fig. 8. Three *adherent-7* plants at the matured stage, right two of which are linked with the *dwarf-10* character and the other not associated with it.

Plate XIII

Fig. 9. An *anther ear-3* plant at the flowering stage.
Fig. 10. A seedling of *anther ear-3*.
Fig. 11. A seedling with *adherent-5* showing the adherent nature at this stage only.
Fig. 12. The leaves with *dead leaf margins-2*, (right two) and normal leaf (left).
Fig. 13. Upper part of a *hairy sheath-2* plant associated with the *wheat tassel* (*wt*).
Fig. 14. A culm with a part of the hairy sheath in an extreme case.
Fig. 15. *sensitive japonica-1* plants reveal phenotypic change by the temperature after being transplanted from the green house to the field.
Fig. 16. The leaves showing the *yellow iojap striping* of various degrees.
Fig. 17. Ear-bearing portion of an *anther ear-3* plant (Fig. 9) showing a typical anther ear character.

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