A genic survey of heritable characters in maize

I. Some new mutants

By

T. SUTÔ, Y. KATÔ and N. MUKAIGAWA

(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 certified 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 work 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-
ficiency (Sutô, 1948a and 1949), (3) the cytoplasmic effect on the pheno-
typic expression of an old gold stripe controlled by a recessive gene,
og (Sutô, 1949 and 1950a), (4) disturbed segregations due to the
dominant gametophytic genes and the lethal genes (Sutô, 1948b and
1950b), (5) the pseudo-allelic nature of some members of a P-allelic
series (Sutô, 1951), (6) the specific nature of two dominant genes,
P"ne", and Tp, affecting the character expression (Sutô, 1948c 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
F₂ 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-f₁-bm₂, II) lg₁-gl₁-v₁,
III) ts₁-lg₁-na₁-a₁, IV) su₁-la, V) bm₁-pr₁-v₁, VI) Pl-sm-py, VII) ra₁-gl₁-Tp-
j₁, IX) ms₃-j₁, IX) c-sh-wx, and X) li₁-g₁-R. Of those marker genes,
six, viz., br, f₁, bm₁, na₁, v₁, 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-E₁₂l" instead of the
"br-f₁-bm₂" has since 1941 been used as a tester of the 1st linkage group,
on the genetical ground that the locus of P and E₁₂l on chromosome
1 is decided with certainty (Sutô 1951).

All of the data were treated statistically by Mather's method of
χ² to test the segregation ratio and the linkage relation. Firstly, an
attempt was made to determine whether or not the observed segre-
gation of giving genes is in accord with the hypothetical one expected
from the Mendelian basis when judged by the calculated value of χ².
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 \( \chi^2 \) analysis of genes involved in Table 1 is given in Table 2. The \( \chi^2 \) 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 \( \chi^2 \), as can be seen in the segregation of genes such as \( ij \), \( ad_s \), \( ys \), \( su \), \( Hs \), \( cr \) and \( ut \). 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 \( ad_s \)- and \( ys \)- 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 established 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, \( dm_s \), \( Hs \), \( cr \) and \( ut \), 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 \( \chi^2 \) for both the segregation and the linkage were computed.
A genic survey of heritable characters in maize

\[ \text{Table 1} \]

Summary of linkage data

<table>
<thead>
<tr>
<th>Genes</th>
<th>Linkage Phase</th>
<th>XY</th>
<th>xY</th>
<th>xy</th>
<th>Total</th>
<th>Recombinations</th>
<th>Linkage group</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>p(%)</td>
<td>sp(%)</td>
</tr>
<tr>
<td>( v_{2} \times j_{1} )</td>
<td>CS</td>
<td>140</td>
<td>41</td>
<td>32</td>
<td>23</td>
<td>236</td>
<td>32.784</td>
</tr>
<tr>
<td></td>
<td>RS</td>
<td>155</td>
<td>65</td>
<td>69</td>
<td>19</td>
<td>308</td>
<td>41.199</td>
</tr>
<tr>
<td></td>
<td></td>
<td>136</td>
<td>69</td>
<td>55</td>
<td>9</td>
<td>258</td>
<td>31.145</td>
</tr>
<tr>
<td>( y_{23} \times i_{j} )</td>
<td>RS</td>
<td>264</td>
<td>93</td>
<td>64</td>
<td>2</td>
<td>423</td>
<td>38.489</td>
</tr>
<tr>
<td>( y_{23} \times r_{a_{1}} )</td>
<td>RS</td>
<td>270</td>
<td>85</td>
<td>82</td>
<td>21</td>
<td>458</td>
<td>38.489</td>
</tr>
<tr>
<td>( g_{23} \times l_{g_{1}} )</td>
<td>RS</td>
<td>128</td>
<td>69</td>
<td>55</td>
<td>9</td>
<td>258</td>
<td>40.455</td>
</tr>
<tr>
<td>( h_{3} \times g_{1} )</td>
<td>RS</td>
<td>252</td>
<td>49</td>
<td>45</td>
<td>12</td>
<td>244</td>
<td>38.489</td>
</tr>
<tr>
<td>( ad_{4} \times l_{g_{1}} )</td>
<td>RS</td>
<td>119</td>
<td>44</td>
<td>45</td>
<td>2</td>
<td>213</td>
<td>38.489</td>
</tr>
<tr>
<td>( ad_{5} \times v_{2} )</td>
<td>RS</td>
<td>267</td>
<td>91</td>
<td>67</td>
<td>5</td>
<td>439</td>
<td>39.558</td>
</tr>
<tr>
<td>( ad_{5} \times b_{m_{1}} )</td>
<td>RS</td>
<td>274</td>
<td>52</td>
<td>33</td>
<td>2</td>
<td>361</td>
<td>34.273</td>
</tr>
<tr>
<td>( ad_{5} \times g_{1} )</td>
<td>CS</td>
<td>262</td>
<td>61</td>
<td>42</td>
<td>39</td>
<td>394</td>
<td>32.813</td>
</tr>
<tr>
<td>( ad_{5} \times d_{10} )</td>
<td>CB</td>
<td>125</td>
<td>21</td>
<td>21</td>
<td>17</td>
<td>284</td>
<td>21.100</td>
</tr>
<tr>
<td>( a_{n_{3}} \times l_{g_{1}} )</td>
<td>RS</td>
<td>202</td>
<td>84</td>
<td>76</td>
<td>16</td>
<td>378</td>
<td>40.455</td>
</tr>
<tr>
<td>( a_{n_{3}} \times l_{g_{1}} )</td>
<td>CB</td>
<td>11</td>
<td>13</td>
<td>17</td>
<td>12</td>
<td>53</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>19</td>
<td>20</td>
<td>14</td>
<td>12</td>
<td>65</td>
<td></td>
</tr>
<tr>
<td>( m_{a} \times i_{j} )</td>
<td>RS</td>
<td>184</td>
<td>54</td>
<td>85</td>
<td>12</td>
<td>325</td>
<td>38.489</td>
</tr>
<tr>
<td></td>
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<td>107</td>
<td>34</td>
<td>49</td>
<td>2</td>
<td>192</td>
<td>38.489</td>
</tr>
<tr>
<td>( m_{a} \times g_{l_{1}} )</td>
<td>RS</td>
<td>182</td>
<td>76</td>
<td>96</td>
<td>10</td>
<td>364</td>
<td>31.145</td>
</tr>
<tr>
<td>( m_{a} \times l_{a} )</td>
<td>RS</td>
<td>350</td>
<td>90</td>
<td>104</td>
<td>6</td>
<td>550</td>
<td>30.951</td>
</tr>
<tr>
<td>( m_{a} \times s_{u_{1}} )</td>
<td>RS</td>
<td>337</td>
<td>93</td>
<td>97</td>
<td>3</td>
<td>350</td>
<td>22.802</td>
</tr>
<tr>
<td>( d_{m_{2}} \times b_{m_{1}} )</td>
<td>RS</td>
<td>409</td>
<td>108</td>
<td>48</td>
<td>11</td>
<td>576</td>
<td>48.003</td>
</tr>
<tr>
<td>( H_{s_{2}} \times c_{r} )</td>
<td>RS</td>
<td>65</td>
<td>103</td>
<td>59</td>
<td>59</td>
<td>296</td>
<td>75.759</td>
</tr>
<tr>
<td>( H_{s_{2}} \times w_{t} )</td>
<td>RS</td>
<td>74</td>
<td>138</td>
<td>40</td>
<td>54</td>
<td>306</td>
<td>45.482</td>
</tr>
<tr>
<td>( c_{r} \times w_{t} )</td>
<td>CS</td>
<td>126</td>
<td>86</td>
<td>42</td>
<td>63</td>
<td>316</td>
<td>69.451</td>
</tr>
</tbody>
</table>

* 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 \( \chi^2 \) analysis

<table>
<thead>
<tr>
<th>Genes</th>
<th>Linkage phase</th>
<th>( \chi^2_X )</th>
<th>( \chi^2_Y )</th>
<th>( \chi^2_L )</th>
<th>Kinds of ( \chi^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( v_21 ) ( \cdot j_1 )</td>
<td>CS</td>
<td>3.416</td>
<td>1.226</td>
<td>20.524 **</td>
<td>Total Deviation</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.714</td>
<td>0.001</td>
<td>25.272 *</td>
<td>Heterogeneity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.702</td>
<td>1.229</td>
<td>2.252</td>
<td></td>
</tr>
<tr>
<td>( v_22 ) ( \cdot l_3 )</td>
<td>RS</td>
<td>2.108</td>
<td>1.398</td>
<td>8.492 *</td>
<td>Total Deviation</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.651</td>
<td>1.246</td>
<td>7.697 *</td>
<td>Heterogeneity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.427</td>
<td>0.147</td>
<td>0.795</td>
<td></td>
</tr>
<tr>
<td>( y_92 ) ( \cdot j_1 )</td>
<td>RS</td>
<td>19.922 *</td>
<td>1.457</td>
<td>9.383 *</td>
<td></td>
</tr>
<tr>
<td>( y_92 ) ( \cdot r_1 )</td>
<td>RS</td>
<td>2.917</td>
<td>1.457</td>
<td>20.741 *</td>
<td></td>
</tr>
<tr>
<td>( g_93 ) ( \cdot l_3 )</td>
<td>RS</td>
<td>1.540</td>
<td>0.841</td>
<td>0.423</td>
<td></td>
</tr>
<tr>
<td>( l_7 ) ( \cdot g_1 )</td>
<td>RS</td>
<td>2.799</td>
<td>1.518</td>
<td>0.628</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.536</td>
<td>0.710</td>
<td>0.499</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.563</td>
<td>0.888</td>
<td>0.134</td>
<td></td>
</tr>
<tr>
<td>( a_4 ) ( \cdot l_3 )</td>
<td>RS</td>
<td>0.265</td>
<td>0.452</td>
<td>5.534 *</td>
<td></td>
</tr>
<tr>
<td>( a_5 ) ( \cdot v_2 )</td>
<td>RS</td>
<td>15.639 *</td>
<td>1.640</td>
<td>6.693 *</td>
<td></td>
</tr>
<tr>
<td>( a_5 ) ( \cdot b_3 )</td>
<td>RS</td>
<td>45.096 *</td>
<td>19.414 *</td>
<td>0.421</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(9.059) *</td>
<td>(0.000)</td>
<td>(5.109) *</td>
<td></td>
</tr>
<tr>
<td>( a_6 ) ( \cdot g_1 )</td>
<td>CS</td>
<td>4.146 *</td>
<td>0.030</td>
<td>24.376 *</td>
<td></td>
</tr>
<tr>
<td>( a_7 ) ( \cdot d_3 )</td>
<td>CB</td>
<td>0.225</td>
<td>0.225</td>
<td>140.845 *</td>
<td></td>
</tr>
<tr>
<td>( a_9 ) ( \cdot l_3 )</td>
<td>RS</td>
<td>0.088</td>
<td>0.004</td>
<td>5.278 *</td>
<td></td>
</tr>
<tr>
<td>( a_9 ) ( \cdot l_3 )</td>
<td>CB</td>
<td>0.072</td>
<td>0.185</td>
<td>1.063</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.542</td>
<td>0.186</td>
<td>0.847</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.530</td>
<td>0.049</td>
<td>0.216</td>
<td></td>
</tr>
<tr>
<td>( m_9 ) ( \cdot r_1 )</td>
<td>RS</td>
<td>3.045</td>
<td>9.016 *</td>
<td>14.090 *</td>
<td>Total Deviation</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.672</td>
<td>8.957 *</td>
<td>19.072 *</td>
<td>Heterogeneity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.373</td>
<td>0.059</td>
<td>1.008</td>
<td></td>
</tr>
<tr>
<td>( m_9 ) ( \cdot q_1 )</td>
<td>RS</td>
<td>3.297</td>
<td>0.366</td>
<td>18.173 *</td>
<td></td>
</tr>
<tr>
<td>( m_9 ) ( \cdot l_1 )</td>
<td>RS</td>
<td>7.388 *</td>
<td>16.701 *</td>
<td>4.533 *</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(2.722)</td>
<td>(0.000)</td>
<td>(31.241) *</td>
<td></td>
</tr>
<tr>
<td>( m_9 ) ( \cdot s_1 )</td>
<td>RS</td>
<td>13.686 *</td>
<td>16.701 *</td>
<td>7.123 *</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.222)</td>
<td>(0.000)</td>
<td>(32.532) *</td>
<td></td>
</tr>
</tbody>
</table>

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 \( \chi^2 \) analysis for the segregation of \( d_{m9} \cdot b_{m1}, H_{81} \cdot cr, H_{82} \cdot wt \) and \( cr \cdot wt \) are neglected here (see text).

Nextly, a profitable approach to the linkage detection was also obtained by an analysis of \( \chi^2 \), essentially similar to that appropriate to the segregation test of individual gene. A significant value of the linkage \( \chi^2 \) 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 $\chi^2$ 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* ($v_{21}^v$ and $v_{21}^f$)**, IIX***

$v_{21}^v$ was found in an inbred line (S–119) of a commercial variety "Longfellow" which was furnished by Hokkaido Agricultural Experiment Station, and $v_{21}^f$ 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 $v_{21}^v$ character is strongly influenced by the low temperature; $v_{21}^v$-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 ($v_{21}^f$) 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; $v_{21}^f$ reveals a typical virescent character while $v_{21}^v$ appears to become normal green.

The phenotype of $F_1$ hybrids between $v_{21}^v$ and $v_{21}^f$ 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 $v_{21}^v$. 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 \( v_1 \) nor \( v_2 \), and (2) in the \( F_2 \) segregation, the \( v_1 \)-plants are a little more numerous than the \( v_2 \). A conclusion may be reached from those findings that the present two genes, \( v_1 \) and \( v_2 \), should be considered to belong to a multiple allelic series; the genetic relation of \( v_1 \) to \( v_2 \) 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 \( v_1 \) hybrid and 221 of the \( v_2 \) 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, \( v_2 \), has its locus on chromosome 8 (Sato, 1946), and a mean value of the recombination between \( v_2 \) and \( j \) was estimated to be ca. 33\% from the two coupling families, one of which came from a \( v_1 \) hybrid and the other from a \( v_2 \) hybrid.

2) virescent seedling-22 (\( v_1 \) and \( v_2 \)), II.

Both mutants (\( v_1 \) and \( v_2 \)) came from inbred lines, S-239 and S-299 respectively, which were derived from a commercial flint variety, "Onao" 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; \( v_1 \)-seedlings are yellowish-white owing to complete lack of chlorophyll while \( v_2 \)-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 \( v_1 \) cross and 196 green and 62 virescent in a \( v_2 \) cross, with a \( \chi^2 \) of
The 1.393 and 1.246 respectively. The F1 character in the cross between \( v^a \) and \( v^b \) is intermediate in color. But, the phenotypic expression on yellowing of color in F1 plants is not so much affected by temperature as in \( v^a \). Accordingly, \( v^a \) and \( v^b \) may be concluded to form a multiple allelic series of genes, and, if so, \( v^b \) must be dominant to \( v^a \) on the temperature effect, but incompletely recessive on other virescent nature.

The locus of \( v^a \) is in chromosome 2 as indicated by the linkage data; \( v^a \) and \( l_g \) are loosely linked together with about 41±3% 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 \( v^a \) 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 (ys3)**, 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 (ys1)** 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 disturbed segregations are sometimes found in crossing progenies owing to the bad viability. For example, a segregation comprising 357
normal and 66 \( y_{s_3} \) 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 \( y_{s_3} \) 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 \( y_{s_3} \) to be on chromosome 7; a recombination value of \( y_{s_3} \) was calculated to be about 20\( \pm \)5\% to \( i_j \) and to be about 30\( \pm \)4\% to \( r_a \). 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 \( "r_a-i_j-y_{s_3}" \) on chromosome 7.

4) green stripe-3 \( (g_{s_3}) \), II (?), Fig. 4.

This mutant was found in one \( (S-818) \) 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 visible 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 leave have usually a tendency to roll and to wilt under the bright sunlight condition of midsummer field.

\( g_{s_3} \) was reported by SUTO (1946) to be simple recessive to normal, and to be loosely linked to \( l_g_i \), which belongs to the 2nd linkage group, the recombination value being estimated at about 40\%. There appears to be a linkage relation between them in the present case too, as well as in the previous case. Actually, a recombination value of approximately 47\( \pm \)3\% can be estimated from a total of 458 plants in the repulsion phase of \( F_2 \) segregation. It may be demonstrated however from \( \chi^2 \) analysis on the linkage relation that \( g_{s_3} \) and \( l_g_i \) should be independent genetically with characters inherited according to an expected ratio of 9:3:3:1 in the \( F_2 \) segregation, because a value of \( \chi^2 \) calculated as 0.428 is statistically not significant.
5) lineate-2 (li₂), 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 Hokkaido 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.

Sutō (1946) reported already that the lineate-2 is inherited as a simple recessive character and is loosely linked to glf, giving a recombination value of about 48% in the repulsion phase of a F₂ segregation. An apparently similar finding was found in the present data, from which a recombination value can be calculated as about 47±4%, if it is estimated. Since a $\chi^2$ for the linkage relation of li₂ to gl is not significant ($\chi^2 = 0.633$), an actual deviation from the 50%-recombination, 3%, may be so negligible as to be non-significant. From the non-significance of a heterogeneity-$\chi^2$ (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 li₂ to gl.

This mutant (li₂) differs evidently from the lineate-1 (li₁) 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 gl locus (Sutō, 1950 a).

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

This mutant occurred in an inbred line, S-25I, from a very early variety of flint corn, "Kiwase", furnished by the Hokkaido Agricultural 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 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 Suto (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 genes are as follows: 31±5\% to \( gl \), and 35±4\% to \( ij \) in 7th linkage case while it is 23±5\% to \( la \) and 17±5\% to \( su \), in 4th linkage case. A linear arrangement of those genes may be therefore given as “\( ij-gl-la-ma \)” and “\( su-la-ma \)” 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''), 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'' and ij'' respectively, both falling into the same locus on chromosome 7 (SUTÔ, 1946). Actually, the F1 plant from a cross between the white and yellow iojap plants was of the same pure yellow stripe as the latter parent. An F2 population involving a total of 96 plants segregated into 72 ij'', and 24 ij'', this being in agreement with the expected 3:1 frequency ratio. The genetic behavior of ij'' is entirely in accordance with that of the white iojap (ij'') except for the color difference of striping.

8) yellow japonica-I (jj'), IIX.

The yellow japonica was discovered as a mutant of the gene marker stock (jj) 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 japonica 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 F2 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*) have been given by Suto (1946) the gene symbols, \( j^w \) and \( j^y \) respectively, falling into an allelic series.

9) *sensitive japonica-1* (*j^w*), 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 \( j^w \), considering it as a member of the *j*-allelic series. \( j^w \) is dominant over \( j \) 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 Hokkaido 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 genic survey of heritable characters in maize

a gene, \( ad_J \). The segregation data indicate that \( ad_J \) is linked to \( l_g \), with about \( 33 \pm 6\% \) of recombination in the repulsion phase of \( F_2 \) segregation.

11) \( ad\text{-}5 \) (\( ad_J^5 \) and \( ad_J^3 \)), '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 Hokkaidó Agricultural Experiment Station, and is characterized by the strongly inhibiting nature of adherence in seedlings (Fig. 11).

\( Ad\text{-}1 \) (Kemiton 1920), \( ad\text{-}3 \) (Eyster 1934) and \( ad\text{-}5 \) 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 \( ad_J^x \). A different type of adherences occurred in the pedigree cultures of \( ad_J^x \)-stocks, discriminating the latter from the former in the less adherence of seedlings; for the latter the gene symbol was designated as \( ad_J^3 \). The F₁ plants from a cross made between \( ad_J^5 \) and \( ad_J^3 \) are of the \( ad_J^3 \) nature in phenotype, and their F₂ segregations were found to occur in a 3:1 ratio in a total of 83 plants, of which 56 are of \( ad_J^3 \)-type and the remaining 27 of \( ad_J^5 \)-type. Accordingly, \( ad_J^5 \) and \( ad_J^3 \) 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 \( ad_J^5 \) and \( bm \), and the other one between \( ad_J^3 \) 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 \( ad_J \) is located on chromosome 5 and its linear sequence is given as “\( bm_1\text{-}ad_J\text{-}v_2 \)”, because the map distance between \( bm \) and \( v_2 \) has been definitely established to be 66 units (Rhoades, 1950).

12) \( ad\text{-}6 \) (\( ad_J \)), 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 $ad_5$ 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 $ad_5$ and $q_1$.

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 Hokkaido 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 amongst all the heritable adherences. Frequently, the adherence is so firmly 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 $ad_i$ and $ad_j$ 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 (an₃), II, Figs. 3, 9, 10, and 17.

The two mutants by the same gene termed as an₃ were found independently in two different inbred lines, of which one, S-152, was isolated from the "Sapporo-Hachigyo" variety of early flint corn and the other one, S-296, from the "Yellow Dent" variety of medium dent corn. Both varieties were supplied by the Hokkaido 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 remarkable 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 F₂ repulsion data that this mutant is inherited as a simple recessive character and hence the gene determining it is to be termed as "an₃"; also it may have its locus in chromosome 2. The existence of such a linkage relation between an₃ and lg, may be further supported by the present data of the same F₂ segregation. Then, $\chi^2$ 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 $\chi^2$ is 1.063 and its heterogeneity $\chi^2$ 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 $an_m$, 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 “Daichi-ou” variety which has originated in northern China, supplied by the Hokkaido 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 “$dm_i$”, and may be very loosely linked to $bm_i$ judging from a $\chi^2$ 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 “Shiro-hazekibi” variety was cultivated, furnisded by the Hokkaido 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.
A genic study of heritable characters in maize

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 $H_s$, $c_r$, and $w t$ (Sutō, 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 $\chi^2$ 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), $H_s$ is similar to $H_S$ in general appearance but differs in pubescent nature, in regard to which $H_s$ 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 $c_r$ and $c_r$), 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) 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: \( v_{22}, g_{85},? , a_{d}, a_{n}, \) on chromosomes 2; \( m_{a} \) on chromosomes 4 and 7; \( a_{d} \) and \( d_{m} \) on chromosome 5; \( g_{8}, j_{f} \) on chromosome 7; \( v_{21}, j_{f} \) and \( j_{f} \) on chromosome 8; \( l_{i}, a_{d} \) on chromosome 10. Further, of the remaining five, two, \( d_{z} \) and \( d_{w} \), and three, \( c_{r}, H_{s}, \) and \( w_{t} \), are linked together independently to one another but their loci on the chromosomes are not yet known.

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A genic survey of heritable characters in maize


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 χ² 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 (bln, blr, blr, blr and blr).

Fig. 3. A semi-dwarf type of anther ear-3 plants.

Fig. 4. An adult plant having green striped leaves (gs) linked with liguleless-1 (lg) (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 greenhouse 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.
T. Sutô Y. Katô and N. Mukai-gawa; A genic survey of heritable characters in maize
T. Sutô, Y. Katô and N. Mukaiwawa; A genetic survey of heritable characters in maize