Beta-ray Induced Chromosome Breakage Phenomena in Plants

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Introduction

X-rays, radium, radiochemicals emitting beta and alpha rays emitted by an external source to living cells for inducing chromosome breaks and rearrangements is well established.

The mutagenic action of radioactive materials absorbed by the cells has been studied on a number of occasions. The resultant transmutation, accompanied by the first recoiling of an atom situated within a gene would sometimes mutate the gene.

Chromosome breaks and rearrangements are produced proportionally to the total dosage of ionization. Sax (1938, 1940 and 1941) and others, namely, Marinelli, Nebel, Giles and Charles (1942) and Thoday (1942) have definitely shown this proportional relationship in Tradescantia.

Observations of Giles (1947), Giles and Lederberg (1948), Giles and Boloney (1948) on Tradescantia and of Arnason, Cummings and Spinks (1948a, 1948b), Arnason (1949) and Ehrenberg, Gustafsson, Levan and U. von Wettstein (1949) on wheat and barley showed that absorbed $P^{32}$ produced large number of chromosome breaks and structural changes. But it was not clear whether the effects were caused by the beta rays located in the chromosomes rendering mutagenic effects. However, Bateman and Sinclair (1950) and King (1952) working on Drosophila found that mutations were produced at a rate beta rays release alone. Hungate and Mannell (1951, 1952) showed that the differences in the mutation rates due to incorporation of radiosulphur, $S^{35}$ were not due to differences in the mutation rates but in the frequency differences of transmutation with the genes. Power (1948) has also observed transmutation in his mutagenic effects of $P^{32}$ in Paramecium. However, Rubin (1948) showed that the mutagenic effects of $P^{32}$ have been greater than the amount of activation and ionization produced in the cells.

The problems related to the structural changes of chromosomes is fundamental aspect of many biological problems. Together with gene muta-

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1 A contribution, in memory of Late Prof. J. B. S. Haldane, F. R. S. the then Senior Research Professor, Indian Statistical Institute, Calcutta-35, while compiling the work with an offer of a Research Fellowship at the Biometrics Laboratory there.

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tion, such changes are the basis of all evolution. The induced chromosome breakage has yielded information on the mode of action of the genes, chromosomes and the cells.

A good number of workers have been studying microsporogenesis in angiosperms where the two meiotic divisions exhibit a high degree of synchrony within an anther.

In radio-isotopes treated cells the ionizations are distributed throughout a longer period till the examination is made at anaphase. Only a fraction of the total dosage from the radioisotopes, therefore, received at these stages alone is capable of producing bridges, fragments on the other hand are produced at all stages of division in the treated cells, and the whole amount of radiation is effective in this case.

A number of workers have turned to microsporogenesis in plants where the meiotic divisions showed a high degree of synchrony. As meiosis is more complex than mitosis and so complications arising from a synapsis and crossing over make study of the aberrations more difficult than the aberrations induced during mitosis.

Linear dose-aberration curve, passing through the original can be examined by the hypothesis that each event observed is a single radiological event or 'hit' (Sax 1938, 1940). But the multiple hit phenomenon such as exchanges are recognized generally to increase as some power of the dose (greater than unity) provided the time of exposure to radiation is same for all cases. However, a single ionizing particle can break only one of the chromatids that must exchange to form a bridge and fragment and thus the bulk breakage will be the resultant of more than one hit. In this experiment, however, the time of exposure given was constant in all the samples and the gross resultant, therefore, considered as multiple hit-phenomenon.

The most adequate means of detecting radiosensitivity is to check the occurrence of fragments and their frequency. A large number of literature showed the cytogenetic effects of ionizing radiation, viz., X-rays, gamma rays, neutrons and various radioisotopes. A complete bibliography on the effects of ionizing radiations on plants (1896–1955) has been recently published by Sparrow, Binnington and Pond (1958) from Brookhaven National Laboratory, U.S.A.

However, the significance of occurrence of the bridge and fragment at anaphase was first investigated and explained by McClintock (1933) in irradiated Zea mays as cytological evidence for crossing-over in the inverted segment. Richardson (1936) has given a full analysis of the various types of cross-overs that can occur in the inverted region as well as proximal to it in relation to types of bridges formed. A first division dicentric bridge and an acentric fragment can arise from:

i) a single chiasma in inversion

ii) two chiasma in the inverted region with one chromatid involved in
both cross-overs and

iii) one cross-over inverted with one proximal to the inversion and chromatid relationships are the same; two chromatids involved in both the cross-overs and the chromatids involved are different in the two cross-overs.

Following ionization, an effect that has been much more frequently observed, is the abnormal distribution of chromatids to the daughter nuclei. The term 'nondisjunction' is applied in this case. In these cases an equal number of cells is formed with extra and with missing chromosomes, respectively, giving rise to changes in the ploidy. Both the extra number and missing of a chromosome involve drastic changes from the normal gene ratios. The imbalanced genetic composition, which is designated as aneuploid, therefore, damages cells functioning.

Fragments with dicentric isochromosome pulled towards opposite poles making bridge and theacentric fragment remaining in the spindle and failing to be pulled towards opposite poles for absence of centromere shows a single chromosome with a single break and the configurations in the following stages, doubling of the chromatids and joining of them to form acentric and dicentric isochromosomes. If the bridges break again by tension dicentric isochromosome results again followed by same type of bridge and its continuation until it is lost.

However, with a view to those, much interest was given in studying configurations showing bridges, their origin, types and their presence with fragments. Also from these, number of breaks in a chromosome were assumed. Stress for finding out the effect of radiosensitivity on the chromosomes given in scoring aberrations in metaphase and early anaphase stages and in general aberrations tabulated were: a) fragments, b) early separation, c) bridges, d) nondisjunctions, e) stickiness and f) late separation.

In this paper, the cytological effects of beta rays from P$^{32}$ and S$^{35}$ are reported.

**Materials and methods**

Experiments on cytological effects induced by radioactive phosphorus (P$^{32}$) and sulphur (S$^{35}$) with half lives of 14.2 and 87.2 days, respectively, procured from Radiochemistry and Isotope Division, Atomic Energy Establishment, Trombay, have been carried out, using the following plants as test material, *Brassica campestris* L. (2n=20), varieties T10 and T151 respectively. Morphology of the plants noted approximately were: Leaves - dark green, pubescent, amplexicaul, flowers: bright, yellow, large, with slightly overlapping petals, anthers - extrose, pods - long, cylindrical and seed - brown.

The cytology of this species has been previously worked out. At diakinesis and metaphase ten bivalents corresponding to the twenty somatic chromosomes were counted. The whole meiotic process in the species is regular and its pollen is good.
In the tests undertaken, the radioisotopes made available to the germinating seeds were divided into two parts for each variety, having 300 seeds in each lot respectively were 1504.2 mc and 2256.3 mc for 24 hours of P$_2$ in the form of orthophosphate in phosphate buffered isotonic solution, pH 7 with specific activity 1.67 per ml and 1504.3 mc and 2256.3 mc for 24 hours in S$^{35}$ as sodium sulphate in isotonic solution, pH 7 with specific activity 1.67 per ml.

Seeds were soaked for 24 hours in radioisotopes and controls were soaked in distilled water for the same period. Treated seeds were thoroughly washed and sown in lines representing each treatment guarded by lines of control seeds. Flower buds were fixed in acetoalcohol between 8 A.M. to 10 A.M. and stored in 70% alcohol and the microsporocytes were smeared in 0.5% carmine. Sometimes ferric chloride in acetic acid was used along with the fixative for ironing. Suitable plates were photographed with the magnification of $\times$2000 representing aberrations induced. Sample size in each treatment taken was 200 cells.

Estimates of aberration rates were based on $p = n = n/N$ and S.E. was calculated from the formula $\sqrt{p(1-p)/N}$ where estimates of aberration rate $= p$, $n =$ number of aberrations observed and $N =$ Total number of observations. Significance of probability of nature of abnormalities in each variety was calculated by estimating $\chi^2$ test with $p$ at 5% = 0.942. $\phi$ was also considered as proportion of abnormalities to the total confidence limits (true value in the range of) under 95% probability.

It is evident from normal sampling that the original population is distributed normally and therefore means are also distributed normally. This fact enables in finding out with the help of the normal probability integral table the limits within which any given population of the sample means lie. Thus, 95% of the means in samples of $n$ lie between the limits $\pm 1.96 \sqrt{n}$ being the population mean or that there is 95% probability that the sample mean lies within these limits. Conversely, if $m$ is the sample mean, the limits $m \pm \frac{1.96}{\sqrt{n}}$ would contain the population mean on an average in 95% of probability is calculated as $p \pm 1.96 \sqrt{p(1-p)/n}$ from the percentage of abnormalities in cells.

Estimates of sampling error in % was also calculated in determining the appropriate sample size in these types of investigations from $\frac{100 \sqrt{n}}{T}$, where $n =$ total number of aberrations observed and $T =$ total number of cells an estimate of sampling error.

Result

Meiotic metaphase and anaphase stages were studied in detail in anthers
obtained from the flower buds from control and beta ray (P³² and S³⁵) irradiated plants of both the varieties of Brassica campestris L. for explaining the possible mechanism for the induction of structural changes in the chromosomes.

Determination of fragments and bridges gave a more adequate estimate
of the frequency of induced aberrations than had been possible with methods previously used. The occurrence of these also indicated the frequency of inversions and number of breaks occurred and configurations of isochromatids thereby.

The fragments which often formed were very small, single and small rods occurred in singly and rarely in pairs. The fragments, in almost all the cases being acentric were found in the spindle (Fig. 1). These probably have occurred during the formation of dicentric bridges after a single hit in one whole chromosome. But since appearance of the fragments often decreased or exceeded the number isochromatid interchange bridges, their origin in addition have been considered to be due to simple, terminal deletions. Cells with fragments or configurations indicating translocations, inversions or deficiency also occurred singly among normal cells, however. Due to very small size of the fragments, attempts were not made in determining the presence of centromere in them. The breakage of chromosomes became evident generally at metaphase except in a few cells where highly fragmented nuclei occurred which seemed incapable of organising a recognisable metaphase. The degree of breakage was extreme and accurate analysis of breakage reunion became impossible in all but a few cells. Difficulty of anaphase separation might be a consequence of obstructed reproduction of chromosomes. Chromosome contraction was semimitotic. There was no evidence of chiasma formation; hence, univalents or centric laggards divided at the first division. Table 1 showed that maximum number of fragments (14) occurred in treatment 1504.2μC of P32 for 24 hours and no fragment in T10 control.

The bridges appeared in various configurations were commonly sticky bridges, delayed separation of chromatids and the interchange bridges. However, most of the bridges derived were due to single break giving an acentric and a dicentric isochromosome, respectively. The dicentric chromosomes, pulled to both opposite poles often formed chromatin bridges at the next anaphase observed. Thus irradiation during interphase gave few structural changes, and mainly were chromatin bridges with their complements, lagging acentric fragments, while translocations, large deletions, and large inversions were rarey found.

Greater damage to tissues were determined by scoring nondisjunctions or lagging of the whole chromosomes. These were commonly due to abnormal distribution of chromatids to the daughter nuclei. Nondisjunctions were considered those chromosomes where the two chromatids that had doubled for mitosis were carried to the same poles. Maximum number of nondisjunctions occurred (17) were under 2256.3μC/24 hrs. in P3 and minimum occurrence (0) was at 1504.2μC/24 hrs.

Apart from the types of aberrations observed and mentioned above, a large number of late metaphase and early anaphase cells were found with
### Table 1. Types of abnormalities

<table>
<thead>
<tr>
<th>Total no. of cells</th>
<th>Variety</th>
<th>Radiochemicals</th>
<th>Treatment μC/24 hr.</th>
<th>Fragment</th>
<th>Bridges</th>
<th>Early separation</th>
<th>Non-disjunction</th>
<th>Stickiness</th>
<th>Late separation</th>
<th>% abnormality</th>
<th>Total no. of abnormal cells</th>
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<tbody>
<tr>
<td>200</td>
<td>T10</td>
<td>Control</td>
<td>Control</td>
<td>0</td>
<td>1</td>
<td>3</td>
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<td>2</td>
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<td></td>
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<td>2256.3</td>
<td>10</td>
<td>25</td>
<td>30</td>
<td>17</td>
<td>14</td>
<td>54</td>
<td>75.00</td>
<td>150</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<td>14</td>
<td>0</td>
<td>19</td>
<td>18</td>
<td>36.00</td>
<td>76</td>
</tr>
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<td>12</td>
<td>43</td>
<td>28</td>
<td>38</td>
<td>10</td>
<td>72</td>
<td>82.50</td>
<td>165</td>
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<td>16</td>
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<td>15</td>
<td>23</td>
<td>17</td>
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<tr>
<td></td>
<td>T151</td>
<td>Control</td>
<td>Control</td>
<td>3</td>
<td>5</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>9.00</td>
<td>18</td>
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<td>P&lt;sub&gt;3&lt;/sub&gt;</td>
<td>2256.3</td>
<td>7</td>
<td>20</td>
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<td>28.50</td>
<td>57</td>
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<td>10</td>
<td>5</td>
<td>4</td>
<td>22.50</td>
<td>45</td>
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<td>2256.3</td>
<td>9</td>
<td>12</td>
<td>15</td>
<td>20</td>
<td>23</td>
<td>17</td>
<td>32.50</td>
<td>65</td>
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<td></td>
<td></td>
<td></td>
<td>1504.2</td>
<td>3</td>
<td>25</td>
<td>7</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>20.50</td>
<td>41</td>
</tr>
</tbody>
</table>

### Table 2. Showing sampling error in % estimation of aberration rate with S.E. and the confidence limit under 95% probability

<table>
<thead>
<tr>
<th>Total no. of cells (N)</th>
<th>Variety</th>
<th>Radiochemical</th>
<th>Treatment μC/24 hr.</th>
<th>Sampling error in %</th>
<th>Estimate of aberration rate (P)</th>
<th>S.E. of P±</th>
<th>Confidence limit under 95% probability</th>
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</thead>
<tbody>
<tr>
<td>200</td>
<td>T10</td>
<td>Control</td>
<td>Control</td>
<td>2.50</td>
<td>0.06</td>
<td>0.312</td>
<td>0.06±0.1356</td>
</tr>
<tr>
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<td></td>
<td>P&lt;sub&gt;3&lt;/sub&gt;</td>
<td>2256.3</td>
<td>6.00</td>
<td>0.75</td>
<td>0.312</td>
<td>0.75±0.7000</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1504.2</td>
<td>4.00</td>
<td>0.38</td>
<td>0.313</td>
<td>0.38±0.1102</td>
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<td></td>
<td>S&lt;sub&gt;5&lt;/sub&gt;</td>
<td>2256.3</td>
<td>6.50</td>
<td>0.82</td>
<td>0.312</td>
<td>0.82±0.5010</td>
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<tr>
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<td>1504.2</td>
<td>5.00</td>
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<td>0.41±0.1072</td>
</tr>
<tr>
<td></td>
<td>T151</td>
<td>Control</td>
<td>Control</td>
<td>2.00</td>
<td>0.09</td>
<td>0.313</td>
<td>0.09±0.1335</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P&lt;sub&gt;3&lt;/sub&gt;</td>
<td>2256.3</td>
<td>4.00</td>
<td>0.23</td>
<td>0.313</td>
<td>0.23±0.2228</td>
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<td>1504.2</td>
<td>3.50</td>
<td>0.22</td>
<td>0.313</td>
<td>0.22±0.1236</td>
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<td></td>
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<td>S&lt;sub&gt;5&lt;/sub&gt;</td>
<td>2256.3</td>
<td>4.00</td>
<td>0.32</td>
<td>0.313</td>
<td>0.32±0.1154</td>
</tr>
<tr>
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<td></td>
<td></td>
<td>1504.2</td>
<td>3.00</td>
<td>0.20</td>
<td>0.313</td>
<td>0.20±0.1250</td>
</tr>
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### Table 3. Probability of types of aberrations in T10

<table>
<thead>
<tr>
<th>Treatment $\mu$Ci/24 hr</th>
<th>Fragment</th>
<th>Bridge</th>
<th>Early separation</th>
<th>Nondisjunction</th>
<th>Stickiness</th>
<th>Late separation</th>
<th>Row total</th>
<th>Row + column total</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2256.3 (P$<em>{312}$ + $S</em>{313}$)</td>
<td>10 + 12 = 22</td>
<td>25 + 43 = 68</td>
<td>30 + 38 = 68</td>
<td>17 + 10 = 27</td>
<td>14 + 20 = 34</td>
<td>54 + 72 = 126</td>
<td>345</td>
<td>1098</td>
<td>272.00*</td>
</tr>
<tr>
<td>1504.2 (P$<em>{312}$ + $S</em>{313}$)</td>
<td>14 + 3 = 17</td>
<td>28 + 16 = 44</td>
<td>14 + 25 = 39</td>
<td>0 + 15 = 15</td>
<td>19 + 23 = 42</td>
<td>18 + 17 = 35</td>
<td>192</td>
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<tr>
<td>Column total</td>
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<td>113</td>
<td>110</td>
<td>44</td>
<td>78</td>
<td>165</td>
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</tbody>
</table>

* Significant at $P=0.05$ with df=10.

### Table 4. Probability of types of aberrations in T151

<table>
<thead>
<tr>
<th>Treatment $\mu$Ci/24 hr</th>
<th>Fragment</th>
<th>Bridge</th>
<th>Early separation</th>
<th>Nondisjunction</th>
<th>Stickiness</th>
<th>Late separation</th>
<th>Row total</th>
<th>Row + column total</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>3</td>
<td>5</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2256.3 (P$<em>{312}$ + $S</em>{313}$)</td>
<td>7 + 9 = 16</td>
<td>20 + 12 = 32</td>
<td>15 + 20 = 35</td>
<td>7 + 12 = 19</td>
<td>4 + 5 = 9</td>
<td>4 + 7 = 11</td>
<td>122</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1504.2 (P$<em>{312}$ + $S</em>{313}$)</td>
<td>0 + 3 = 3</td>
<td>5 + 25 = 30</td>
<td>21 + 7 = 28</td>
<td>0 + 14 = 14</td>
<td>5 + 1 = 6</td>
<td>4 + 1 = 5</td>
<td>86</td>
<td>452</td>
<td>184.00*</td>
</tr>
<tr>
<td>Column total</td>
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<td>67</td>
<td>67</td>
<td>35</td>
<td>16</td>
<td>19</td>
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<td></td>
</tr>
</tbody>
</table>

* Significant at $P=0.05$ with df=10.
chromatid stickiness and late separation of bivalents and have been tabulated in Table 1.

In Table 1 it has been shown that the aberrations were linearly correlated with the doses and number of aberrant cells found were more in variety T10 than in T151. Also aberrations under radiosulphur treatment were more than that of in radiophosphorus in both the varieties.

Estimating of aberration rates with confidence limit under 95% probability more calculated and it was found in var. T10 with 0.06±0.1356 had higher rate than var. T151 with 0.09±0.1335 and aberrations under radiosulphur treatment had showed much higher rates than the control keeping a linear relationship with the increase of dosages. In Table 3, it has been shown that the probability of types of abnormalities in variety T10 is significantly high with a $\chi^2$ values of 272.00 significant at 5% level with 10 degrees of freedom. Also in case of var. T151 the $\chi^2$ value of probability of aberration was noted to be 184.00, significant at 5% level with 10 degrees of freedom, $p$ value at 5% being 9.342. (Table 4).

However, an analysis of the present data indicated that in both the varieties of B. campestris L. there was an increase in the frequency of the abnormal cells with increase in dosages (Tables 1 and 2) and within the dosages keeping the linearity. Variety T151 appeared to be less susceptible when compared with the other variety, as determined by the number of abnormal cells.

**Discussion**

Effects of ionizing radiations are measured in terms of injury symptoms, cytological aberrations, and mutations. Usually these effects are associated with damage, and increase or decrease are correlated. Induced mutation has been used here in the sense to refer to changes which are transmitted in frequencies comparable to naturally occurring mutations. A mutation would not, therefore, include detectable aberrations, but also would include minute chromosomal changes, especially deficiencies.

Dicentric chromosomes showing bridges have been observed in many cases, but they are usually eliminated within a few cell generations.

An apparent exception to this rule in maize endosperm where dicentrics were still found in many divisions following their inception and a breakage-fusion-bridge cycle was set up (McClintock 1943, 1944) so that the dicentric was broken at each cell division, with sister ends uniting to form new dicentric chromosomes.

At meiosis the two centromeres of the unpaired dicentric chromosome almost always opposed each other during observation, attenuating the intercentromeric region and orienting the region perpendicular to the metaphase plate. Usually the entire chromosome was included within the one telophase group. Occasionally, however, breakage occurred in the intercentromeric
region giving rise to monocentric chromosomes. These breaks were difficult to observe, and not always could be made possible to obtain the accuracy in their recording as, in some of the other types of aberration. But considered so as the origins of configurations like dicentric bridge with an acentric fragment at the spindle. Isochromatid breaks: These aberrations, which Sax termed ‘1-hit chromatid breaks’ involving breaks in both sister chromatids followed by lateral fusion to produce a dicentric chromatid and an acentric U-shaped fragment (sister reunion of Darlington and Upcott 1941).

Chromatid interchanges were found in various degrees of complication, and involved breaks in two (or more) chromatids and reunions in new fashion.

Chromosome breaks: These were scored in accuracy since whole chromosome breaks were quite visible.

Chromosome interchanges, which involved two breaks in the same chromosome giving rise to rings and fragment chromosomes having centromere. Rings noted were rare but centric fragments were frequent and inversions likely to be equally frequent could not be indentified. Between the two chromosomes either eucentric or dicentric interchanges were expected. But practically only the latter type, which resulted in the production of a dicentric chromosome and acentric fragment, were scored regularly.

However, the breaks so formed certainly did not rejoin at random in the nucleus, as had been assumed to be the case of the breakage theory. As regards the production of aberrations neither the contact theory nor the breakage theory could be made wholly right or wholly wrong.

Prolongation of the division after doses longer than those to reduce the count to zero in barley has been reported as a radiation induced retardation in mitotic rate of cells and an increase in the time required by cells passing through anaphase, if the dose is larger to cause stickiness of the chromosomes.

Jungling and Langendorff (1930) found that in the *Vicia* root tips mitosis occurred 18 hrs. after 420 r. and 33 hrs. after 550 r. treatments respectively. Increased doses cause increased delay in the breakdown of the nuclear membrane, increased stickiness of the chromosomes of the *Chortophaga* neuroblast and thereby completion of mitosis is delayed (Carlson 1941a). Similar results were obtained here in beta-ray treatment producing deformed and adherent metaphase and anaphase chromosomes. There results agreed with those of Humes (1950), who found that the ‘stickiness’ of chromosomes caused by the ‘sticky’ gene in maize and by chemical treatment of root tips of onion was not due to depolymerisation of the deoxyribonucleic acid. But in *B. campestris*, normal cells showed that stickiness was rare but increased in treatments.

Lastly, however, percentages of aberrations in different treatments showed proportional effect with the treatments.
Summary

After treatment of two varieties of Brassica campestris L. (2n=20), T10 and T151 with radioactive chemicals P³² and S³⁵, having different concentrations, aberrant cells, for studying the effects were scored in meiosis.

According to the nature of abnormalities in metaphase and early anaphase cytological effects and origin of different abnormal configurations were explained.

Significance of probability of nature of abnormalities was estimated by χ² test and estimate of aberration rates were based on p=n−n/N and S.E. = \( \sqrt{\frac{p(1-p)}{n}} \) was also considered as proportion abnormalities to the total confidence limits. Sampling error was also calculated per treatment in percent to record optimum sample size for analysis.

Linearship between treatments and cytological aberrations was shown.

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References


* Cross references.