84 per cent albite and we know enough of relations in our general system (Fig. 1) to be able to say that the conditions are similar in mixtures with an excess of silica (simplified fayalite-rhyolites) and also in those with a deficiency of silica (simplified fayalite-phonolites). While we have made only a first step in the investigation of these extreme liquids it is plain from the results of this study that the moderate content of iron silicates in rocks rich in alkali feldspars cannot be urged as a feature militating against the acceptance of the rocks as substantially representative of the residual liquids from the fractional-crystallion of more complex "basic" magmas.

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FREQUENCY OF "CELL-LETHALS" AMONG LETHALS OBTAINED AT RANDOM IN THE X-CHROMOSOME OF DROSOPHILA MELANOGASTER

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The work to be reported in this paper is a by-product of experiments conducted in 1933 and 1934 when an attempt was made to determine the phenotype of a deficiency homozygous for certain known loci.[1] Deficiencies involving 12 short regions and including known loci of the *X*-chromosome were tested and in all but one case they were found to be cell-lethal. In the course of this experiment a number of *X*-chromosome lethals which occurred at unselected loci were also tested for the cell-lethal effect. The results of these tests will be described here.

Methods.—All lethals under consideration here were induced by x-ray treatment. All of them are *X*-chromsome lethals. They were picked up at random in the second generation from matings *m Mn f*/*m f* ♀ × x-rayed *y v* ♂.[2] The presence of *y*, *v*, *m* and *f* factors made it possible to test for crossing-over irregularities throughout almost the entire length of the chromosome and thus to determine whether or not a chromosomal abnormality was present. Only those lethals were used here which were free from

chromosomal abnormalities, since it has been found that frequently cell-lethal tests cannot be made if such an abnormality is present.

It has been shown by Bridges[3] that on females heterozygous for *Mn* there frequently appear small patches of wild-type tissue. He interpreted this as being due to the elimination of the *Mn* chromosome in the course of somatic cell divisions. After investigating this problem with somatic minutes, Stern[4] reinterpreted Bridges' results. He presented evidence for the occurrence of somatic segregation of *X*-chromosomes by which twin patches are formed, one patch representing the cell lineage of a cell carrying one *X*-chromosome and the other, the cell lineage of the cell carrying the other *X*-chromosome. Since *Mn* is a cell-lethal, the patch having the *Mn* chromosome only is not formed, and consequently only the patch representing the other homologous chromosome appears. If, therefore, the other chromosome carries a lethal to be tested and that lethal is a cell-lethal, no patches are expected to appear on *Mn/l* flies; if on the other hand the lethal is not a cell-lethal, single patches are expected to show. Stern[4] has shown that during such somatic segregation crossing-over occurs and hence a small number of single patches are produced representing the cell lineage of a chromosome from which the lethal factor has been removed through crossing-over. The test for a cell-lethal effect by this method, therefore, consists in determining the comparative frequency of patches on minute females carrying a lethal and on controls not carrying it. If the frequency of spots on females with a lethal is significantly lower than on the control females, it is assumed that this lethal is a cell-lethal.

It was known at the time of this experiment that such somatic segregation is stimulated by any *X*-chromosome minute. A minute present in the blond translocation was used in this work thus making it easy to introduce into females the lethal to be tested. In the blond translocation, the tips of the first chromosome and the second chromosome are interchanged. If a blond female heterozygous for the translocation is mated to a normal male, about 25 per cent of the female offspring will receive a first chromosome with a translocated second chromosome piece and two normal second chromosomes. Such females will have the end-piece of one of the first chromosomes missing, will have a minute phenotype and will show frequent patches. The procedure adapted in these tests is shown below:

Cross: *dl*–49, *y Hw/l*; +/+ ♀ × Bld^{-1L+2R}; 2^{-2R+1L}/+ ♂

♀ Offspring: (1) *dl*–49, *y Hw*/Bld^{-1L+2R}; +/2^{-2R+1L} = blond, hairy wing

(2) 1/Bld^{-1L+2R}; +/2^{-2R+1L} = blond

(3) *dl*–49, *y Hw*/Bld^{-1L+2R}; +/+ = blond, hairy wing, minute

(4) 1/Bld^{-1L+2R}; +/+ = blond, minute

When a lethal was located in the middle of the chromosome *dl*–49, *yHw* was used as a balancer and as a marker for the chromosome not carrying the lethal; bar was used when a lethal was located in the left-hand end of the chromosome. Mosaic patches were frequent on minute females (3) and (4), (3) serving as controls and (4) as tests. A significantly lower number of patches on (4) females indicated that the lethal tested was a cell-lethal.

When this experiment was almost completed Stern's[4] finding that autosomal minutes also increase the frequency of somatic segregation of the *X*-chromosome became known to me. In that case twin patches are produced on minute flies; one patch representing the cell lineage of one of the *X*-chromosomes and the other the cell lineage of the other *X*-chromosome. If the lethal to be tested is present in one of the *X*-chromosomes and that lethal is a cell-lethal, only one patch will appear where two are expected, and if the lethal is not a cell-lethal, both of the patches will develop. Since this method is more clear cut and, therefore, more dependable than the previous one, some of the lethals were retested by it as a check on the blond-method. The test made with the autosomal *M* method confirmed the results obtained with blond. The procedure followed with the autosomal *M* method is as follows:

Cross: *dl*–49, *y Hw/y l*; +/+ ♀ × *sn*; M_6/+ ♂

♀ Offspring: (1) *dl*–49, *y Hw/sn*; +/+ = hairy wing

(2) *y l/sn*; +/+ = wild-type

(3) *dl*–49, *y Hw/sn*; +/M_6 = hairy wing, minute

(4) *y l/sn*; +/M_6 = wild-type, minute

The females listed under (4) were examined and if twin spots (yellow and singed) were found, that indicated that the lethal was not a cell-lethal.

To avoid any misunderstanding it seems advisable to define the term "cell-lethal" as used here and in other papers. This term stands for a lethal which, when homozygous, prevents the appearance of a small patch of tissue for which the test is made. The term does not imply that the lethal in question has a lethal effect on a single cell. In these experiments tests were made on the hypodermal cells of females. It is possible that some of the lethals which are found to be cell-lethal in these cells are not cell-lethal in some other tissue. An example of that type is available in case of the $(y\ ac\ sc)^{-260-1}$ deficiency[5] which is cell-lethal in the hypodermal cells of females but as indicated by the work of Ephrussi[6] is not cell-lethal in the hypodermal cells of males.

Results.—In table 1, 24 lethals are listed 5 of which were tested by both methods. Ten of them were found to be cell-lethal for the hypodermal cells of females.

Discussion.—The finding that about two-fifths of random lethals are cell-lethals differs markedly from the results obtained with lethals affecting known visible loci. In addition to the loci *w, fa, ct, t-amx, m, wy-s, g-ty, Mo-f, f, B+, Bx, M* and *Mn* mentioned in an earlier paper[7] *y-ac* and *dy* have been subsequently tested and should be added to the list. Out of the lethals involving any of these 15 regions of the chromosome, only the lethals for two regions (*y* and *ct*) were found to be non-cell-lethal. While the proportion of cell-lethals to non-cell-lethals for the random lethals was 10 to 14, this proportion for lethals affecting known loci was 13 to 2. Non-cell-lethals affecting visible loci are, therefore, five times as frequent as among random lethals. Visible loci for which lethals were present in these experiments were not selected for any special characteristic. Those were

TABLE 1

RESULTS OF CELL-LETHAL TESTS OF VARIOUS LETHALS

NO.	LETHAL	NO. OF PATCHES CONTROL	NO. OF PATCHES TEST	BLOND METHOD PERCENTAGES OF PATCHES ON M FLIES CONTROL	TEST	DIFFERENCE	D/P. E.	M6 METHOD PATCHES TWIN	SINGLE
		Cell-lethals							
1	253– 2	67	10	16.1 ± 1.2	3.3 ± 0.7	12.8 ± 1.4	9.2	..	..
2	–12	21	3	12.1 ± 1.7	1.4 ± 0.6	10.7 ± 1.8	6.1	..	..
3	–13	14	4	14.9 ± 2.5	2.9 ± 1.0	12.0 ± 2.7	4.5	..	..
4	–23	..	..	.....	.....	.....	..	..	4
5	–35	..	..	.....	.....	.....	..	..	6
6	–38	14	6	14.0 ± 2.3	4.9 ± 1.3	9.1 ± 2.7	3.4	..	4
7	–40	14	3	13.1 ± 2.2	2.4 ± 0.9	10.7 ± 2.4	4.5	..	..
8	–43	16	4	14.8 ± 2.3	2.9 ± 1.0	11.9 ± 2.5	4.8	..	..
9	–44	21	3	13.6 ± 1.9	2.6	11.1	..	..	..
10	–55	21	9	12.4 ± 1.7	5.26 ± 1.2	7.1 ± 2.1	3.5	..	4
		Not cell-lethals							
11	– 3	19	22	10.9 ± 1.6	11.1 ± 1.5	.....	...	..	..
12	–14	..	..	.....	.....	.....	..	4	..
13	–16	12	14	8.5 ± 1.6	7.1 ± 1.2	1.4 ± 2.0	0.7	..	..
14	–17	..	..	.....	.....	.....	..	4	..
15	–18	15	20	13.2 ± 2.1	13.8 ± 1.9	0.6 ± 2.3	0.2	..	..
16	–19	4	8	10.8 ± 3.4	16.0 ± 3.5	.....	..	4	..
17	–25	..	..	.....	.....	.....	..	4	..
18	–27	6	6	11.5 ± 3.0	10.2 ± 2.7	1.4 ± 4.0	0.4	..	..
19	–28	14	13	8.4 ± 1.5	6.0 ± 2.0	2.4 ± 1.8	1.3	..	..
20	–29	22	11	13.1 ± 1.8	16.2 ± 3.0	3.1 ± 3.5	0.9	3	..
21	–39	..	..	.....	.....	.....	..	6	..
22	–42	..	..	.....	.....	.....	..	3	..
23	–52	10	17	18.9 ± 3.6	25.4 ± 3.6	6.5 ± 5.1	1.3	5	..
24	–51	23	17	16.0 ± 2.1	10.5 ± 1.6	5.5 ± 2.6	2.1	..	..

used for which favorable stock combinations were available at the time of the experiment. They may be taken as representing a random sample of visible loci.

The lethals affecting visible loci are small deficiencies which include in the majority of cases one known locus only. Cytological studies of salivary chromosomes made on a number of these deficiencies show that each of them involves several bands. If each of the bands represents a locus, that suggests that each of these deficiencies involves in addition to the known visible locus several other loci. There is no reason to believe that random lethals are any different from lethals affecting known loci. Probably all or at least a great majority of them are deficiencies. If these lethals are deficiencies, there is again no reason to suppose that they are different from those affect-

ing known loci since both were produced by the same agent. It seems justifiable to assume, therefore, that these two sets of lethals are comparable except for the fact that in one case a known locus is involved and in the other case either no known locus is affected or if it is that fact has not been discovered. If this assumption is granted, the unavoidable conclusion is that the difference in the proportion of cell-lethals observed in these sets is due to the presence in one of deficiencies affecting known visible loci. This would indicate, that, on the average, loci in which genic changes have a visible effect play a more important rôle in the vital processes of an organism that the loci in which genic changes do not show such an effect. As has been mentioned elsewhere[8] there is ample evidence pointing to such a difference between various loci. In some instances, as in the case of notch (facet) and several minutes, a heterozygous deficiency has a striking upsetting effect upon the organism, while in another case a homozygous deficiency involving four bands of the tip end of the *X*-chromosome and presumably involving at least four loci is perfectly viable.

Summary.—Out of the 24 *X*-chromosome lethals produced at random by *X*-rays 10 were found to be cell-lethal in the hypodermal cells of females. These lethals are compared with lethals affecting known visible loci in which 13 out of 15 were found to be cell-lethals. The higher frequency of cell-lethals among lethals affecting visible loci suggests that on the average these loci play a more significant rôle in the vital processes of the organism than do the other loci.

An opinion is expressed that the majority of lethals are probably deficiencies.

[1] Demerec, M., these PROCEEDINGS, **20**, 354–359 (1934).

[2] The following symbols are used in this paper: *ac* = achaete; *amx* = almondex; *B* = bar; *Bld* = blond; *Bx* = beadex; *ct* = cut; *dl*–49 = delta–49 inversion; *dy* = dusky; *f* = forked; *fa* = facet; *g* = garnet; *Hw* = hairy-wing; *l* = lethal; *m* = miniature; *M* = minute; *Mn* = minute-n; *Mo* = minute-o; M_6 = minute-6; *s* = sable; *sc* = scute; *sn* = singed; *t* = tan; *ty* = tiny; *v* = vermilion; *w* = white; *wy* = wavy; *y* = yellow; 1 = first chromosome; 2 = second chromosome; + = wild-type.

[3] Bridges, C. B., these PROCEEDINGS, **11**, 701–706 (1925).

[4] Stern, C., *Amer. Nat.*, **68**, 164–165 (1934); *Ibid.*, **69**, 81–82 (1935).

[5] Demerec, M., and Hoover, M., *Amer. Jour. Hered.*, **27**, 206–212 (1936).

[6] Ephrussi, B., these PROCEEDINGS, **20**, 420–422 (1934).

[7] Demerec, M., *Cold Spring Harbor Symposia on Quant. Biol.*, **2**, 110–115 (1934).

[8] Demerec, M., *Science*, **81**, 420 (1935).