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made on the basis of genetical analysis of the population; in fact, the variability in the reduction of kernel weight due to the effect of opaque-2 was found to be under genetical control ( $h^2 = 0.52$ ), but its amount was not very large when the portion attributable to the multiplicative effect of the gene was removed. However, it must be remembered that the hybrids compared differed in only one parent. Therefore, the differences would probably have been larger if crosses were made between lines selected in the same direction. Moreover, since the pollen has effects on endosperm development, the differences between hybrid values might have been underestimated because each combination was not pollinated by its own pollen.

In many cases it was observed that the reduction of differences between normal and opaque kernels was associated with modification of the endosperm phenotype, which shows visible translucent sectors. It remains to be seen whether this phenomenon changes the chemical composition of the endosperm.

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## Nucleolar patterns in microspore quartets of trisomic 6, in relation to trisomic inheritance.

Trisomic inheritance of the nucleolar chromosome (chromosome 6) was investigated. Microsporocytes collected from trisomic plants were examined in connection with the behavior of the three chromosome 6 units during meiosis. Root tips were collected, and their chromosomes counted, in a sample of individuals obtained from the cross:  $2n+1 \times 2n$ . Comparisons were made of the trisomic 6 frequency (38%) found among the progeny of this cross with the meiotic behavior of the chromosomes present in triplicate. The data indicated that post-meiotic losses of n+1 spores and/or of 2n+1 zygotes or embryos may take place, in addition to meiotic losses, and may partially account for the failure of trisomic types to reach the theoretical frequency of 50% in the progeny.

The finding of post-meiotic losses in this trisomic 6 material contradicts Einset's statement (Genetics 28:349-364, 1943) that failure of the extra chromosome to be transmitted to 50% of the progeny through the egg apparently was due only to its elimination as a univalent during the meiotic divisions. After examining eight primary trisomes, Einset found the <u>n+l</u> spore frequency close to the <u>2n+l</u> seedling frequency following the same type of cross as described above. However, a reexamination of Einset's pooled data shows an excess of <u>n+l</u> spores over <u>2n+l</u> seedlings with a  $\chi^2$  value of 3.5, which corresponds to a P value of 0.06 (very close to the significance level of 0.05). The outcome of the present investigation supports the hypothesis that, after meiosis is completed, some mechanisms may limit trisomic transmission.

A great majority of microsporocytes (86.7%) examined at anaphase I showed a 2-1 segregation of chromosomes 6 to opposite poles. The remaining fraction was about equally distributed for events of univalent predivision (equational division) and univalent lagging followed by loss.

The analysis of the second meiotic division revealed that most chromatids from pre-divided univalents were included in telophase II nuclei (only 2% of telophase II cells showed a laggard, while in nearly 6% of the anaphase I cells the unpaired chromosome was observed to undergo an equational division). The same conclusion is reached after analyzing the nucleolar patterns in microspore quartets:

| Expected frequencies    | Type 1 | Type 2 | Type 3 | Type 4 | Total |
|-------------------------|--------|--------|--------|--------|-------|
| (A)                     | 100    | 0      | 0      | 0      | 100   |
| (B)                     | 86.0   | 1.8    | 7.2    | 5.0    | 100   |
| (C)                     | (17.8) | 49.1   | 32.1   | (1.0)  | 100   |
| Observed<br>frequencies |        |        |        |        |       |
| (D)                     | 20.3   | 32.3   | 46.4   | 1.0    | 100   |

## Where:

- (A) = Theoretical frequency with 100% 2-1 disjunction at anaphase I (no meiotic losses).
- (B) = Approximate expected frequency of nucleolar organizer distribution based on meiotic observations.

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- (C) = Expected frequency of nucleolar distribution, calculated from the expansion of (m+d)<sup>2</sup> (type 4 and type 1 were arbitrarily separated).
- (D) = The observed frequencies based on a population of 3,492 quartets.
- m = frequency of mononucleolate dual organizer spores, calculated as .5662
- d = frequency of dinucleolate dual organizer spores, calculated as .4338

If (D) is compared with (B), type 2 and type 3 are found in excess, at the expense of types 1 and 4. This discrepancy is explained by the tendency of two N.O.'s to develop a single nucleolus, or by the tendency of two nucleoli to become fused into a single structure, due to the proximity of the related chromosome segments.

A comparison of (D) with (C) revealed an excess of type 3 at the expense of type 2. This may be related to trivalent 6 formation, which would be responsible for the proximity of N.O.'s following a 2-1 chromosome 6 segregation at anaphase I. This proximity would be maintained through the second division in most cases.

A study of nucleolar patterns in microspore quartets of tetraploid maize was made by G. Doyle (MNL 44:155-157, 1970) who argued that the mirror image spatial relationship of the chromosomes in the two telophase I nuclei is often lost in the formation of metaphase II plates, which are rotated 90° with respect to the metaphase I plate.

Other less frequent types of microspore quartets with relation to nucleolar distribution were found, but will not be discussed here.

Type 4 quartets resulted, presumably, from pre-divided univalents which were both included in telophase II nuclei, after migrating in opposite directions. This diagonal configuration is peculiar, with regard to the behavior of univalents, to trisomic 6 individuals and, with some modifications, to monosomic 6 individuals (D. F. Weber, personal communication).

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