GENETIC CONTROL OF CHROMOSOME ELIMINATION DURING HAPLOID FORMATION IN BARLEY

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ABSTRACT

Genetic control over chromosome stability in the interspecific hybrid embryos of Hordeum vulgare and H. bulbosum has been hypothesized to reside on specific chromosomes. In this study, crosses between the primary trisomic lines for the seven different H. vulgare chromosomes and tetraploid H. bulbosum revealed that both chromosomes 2 and 3 of H. vulgare were involved in the control of chromosome elimination. Subsequent crosses using the available monotelotrisomics for chromosomes 2 and 3 led to the conclusion that both arms of chromosome 2 and the short arm of chromosome 3 most likely contain major genetic factors. From the results of this study and the genome balance observed in the interspecific crosses between H. vulgare and H. bulbosum at the diploid and tetraploid cytotypes, it appears that the factors causing the elimination of the bulbosum chromosomes are located on the H. vulgare chromosome. These factors are offset or balanced by factors on the H. bulbosum chromosomes which, when present in sufficient dosage, either neutralize the effects of the vulgare factors or are able to "protect" the bulbosum chromosomes.

Most aspects of chromosome behavior are considered to be under genetic control, as are most morphological characteristics (Rees 1961). For example, genetic control has been demonstrated for asynapsis (Beadle 1930, 1933), desynapsis (Li, Pao and Li 1945; Ramage and Hernandez-Soriano 1972), homoeologous chromosome pairing (Riley and Chapman 1958; Sears and Okamoto 1958), chiasmata frequency (Rees 1955; Rees and Thompson 1956) and chromosome morphology (Beadle 1932; Wellwood and Randolph 1957). Furthermore, examples of genetic control of chromosome elimination are available and are very diverse, such as: in the early embryo development of insects (Geyer-Dusznyska 1959); due to the presence of B chromosomes at the second microspore mitosis in maize (Rhoades and Dempsey 1972, 1973); and maternal transmission of chloroplast genes in Chlamydomonas reinhardi (Sager and Ramanis 1973).

In the genus Hordeum, the elimination of H. bulbosum chromosomes from the interspecific hybrid of H. vulgare (cultivated barley) with H. bulbosum is well documented (Kasha and Sadasiviah 1971; Subrahmanym and Kasha 1973) although the mechanism of elimination is not known. The results of all possible

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crosses between the diploid and autotetraploid cytotypes of these two species revealed that chromosome elimination occurred in all genomic combinations, except that it was rare in hybrids with genome ratios of one vulgare to two or more bulbosum genomes. This information and the evidence that the occasional hybrids produced from the cross of tetraploid *H. vulgare* by tetraploid *H. bulbosum* contained 27 (rather than 28) chromosomes led Kasha, Kao and Reinebergs (1970) to hypothesize that elimination might be controlled by specific chromosomes. The objective of this study was to determine if a specific chromosome (or chromosomes) controls the selective or preferential elimination of *H. bulbosum* chromosomes.

**MATERIALS AND METHODS**

The scheme to test the hypothesis of genetic control of chromosome elimination is illustrated in Figure 1. The primary trisomic stocks for seven different *H. vulgare* chromosomes were crossed with pollen from autotetraploid *H. bulbosum*. Since the trisomic plants produce two kinds of gametes, one with 7 and the other with 8 chromosomes, two types of hybrid progeny are expected from such crosses, namely: (1) 21-chromosome triploid hybrids produced when the 7-chromosome gamete is transmitted and (2) 22-chromosome hybrids produced when the 8-chromosome gamete is transmitted. The 21-chromosome hybrids should be similar to the relatively stable hybrids produced from the cross *H. vulgare*(2X) × *H. bulbosum*(4X).

The frequency of 22-chromosome hybrids should be similar to the usual transmission frequency of the extra chromosome through female gametes in trisomic plants. However, if specific chromosomes carry a factor or factors controlling chromosome elimination, the 22-chromosome hybrids will not be expected to survive (or will be rare) in crosses with a plant trisomic for that chromosome. This is because the controlling genes on this chromosome will now be in the ratio of 2V : 2B (see Figure 1) and the bulbosum chromosomes should be eliminated. In such instances, one might expect to find 8 chromosome (2n = X + 1) haploid plants of *H. vulgare* if they are able to survive following chromosome elimination.

Following the results from crosses with primary trisomics that indicated that specific chromosomes were controlling chromosome elimination, *H. vulgare* plants monotelotrisomic for these specific chromosomes were crossed with bulbosum to locate more precisely the arms containing factors exhibiting control over chromosome elimination.

Three clones of tetraploid *H. bulbosum* (Accs. B143, B816 and B830) from T. Rajiathy, Agriculture Canada, Ottawa were used in this study as a pollen source. In addition 23 progeny plants (from open-pollinated seed of these clones) were used in these crosses.

Four different genotypic sources of *H. vulgare* primary trisomics were used: From E. N. Larter, Univ. of Manitoba, Winnipeg, (1) trisomics for all chromosomes except 3 from progeny of OAC 21 × Montcalm cultivars and (2) trisomic 6 from the cultivar Gateway; From R. T. Ramage, Univ. of Arizona, Tucson, (3) trisomics for chromosomes 2 and 3 from the cultivar Betzes; and from T. Tsuchiya, Colorado State Univ., Fort Collins, (4) trisomic 5 in cultivar Shin Ebsin.

Four monotelotrisomic lines in diploid *H. vulgare* were used in this study. One had been identified as being the long arm of chromosome 2 (Telo 2L) and a second as the long arm of chromosome 3 (Telo 3L), although the latter identification may not be as certain (Tsuchiya and Singh 1973). Telo 2C and Telo 2D were found during this study among the progeny of primary trisomic 2 and thus, are most likely monotelotrisomic for one of the arms of chromosome 2. Neither has yet been identified with marker genes but in plant type, Telo 2C resembles Telo 2S and Telo 2D that of Telo 2L as reported by Fedak, Tsuchiya and Helgason (1971) and Tsuchiya (1969, 1972).

Tetraploid *H. bulbosum* plants were placed in a cold chamber (10° with 10-hr day length) for vernalization. After a period of 3 months, plants were removed from the cold chamber and
Figure 1.—Outline of the crosses of primary trisomics of *H. vulgare* (Trisomic 1 for example) with tetraploid *H. bulbosum*. Two types of progeny are produced, one with 21 chromosomes and another with 22 chromosomes. If chromosome 1 of *H. vulgare* controls the elimination of *bulbosum* chromosomes, then the 22-chromosome progeny will become 8-chromosome *H. vulgare* plants, if they are able to survive. V₁ and B₁ represent chromosome 1 of *H. vulgare* and *H. bulbosum*, respectively and so on.

Placed in a growth room (17-hr artificial light day length; temperature 23° ± 1° with lights on and 16° ± 1° during the dark) to obtain pollen. Flowering occurred 3 to 4 weeks after placement of the clones in this growth room.

Trisomic plant florets were emasculated by clipping off the top one-third of the lemma and the palea with scissors and removing the anthers. Two days after emasculation, fresh pollen from tetraploid *H. bulbosum* was collected in a petri dish and immediately applied to the florets with a small brush. Gibberellic acid (GA₃) at a concentration of 75 ppm was added to the florets, 1 drop per day for two successive days after pollination, as described by Subrahmanyan and Kasha (1971).

The young embryos were removed from the immature seeds about 14–16 days after pollination and placed on the culture medium. The culture medium was the B₆ medium described by...
The embryos were incubated at 22°C in the dark. After 1–2 weeks, when visible root and/or shoot initiation had occurred, they were transferred to a growth chamber with 12 hours' photoperiod at 22°C. The seedlings at the 2–3 leaf stage were removed from the vials and potted in a mixture of peat moss, Turface and Perlite (1:1:1), the latter two substances being commercial inorganic materials used for potting plants.

For determining the chromosome numbers of parental and hybrid plants, root-tips were collected and pretreated in cold water (0–2°C) for 18 hours and fixed in acetic alcohol (1:3) for about 30 minutes. The root-tips were then rinsed in distilled water, hydrolyzed in 1N HCl at 60°C for 20 minutes, treated with 1% pectinase at 37°C for 30 minutes and stained with Feulgen. Slides were prepared by the squash technique.

RESULTS

Primary Trisomics

The data on the florets pollinated and the seedlings obtained from crosses between the *H. vulgare* primary trisomics and tetraploid *H. bulbosum* are presented in Table 1. The percentage seed set (29% to 50%) on trisomic plants using bulbosum pollen was lower than that usually obtained on disomic plants (ca. 70%). The number of caryopses that developed embryos ranged from 56% to 77% and the frequency of embryos germinating ranged from 27% to 54%. However, only 10% to 28% of the embryos developed to the seedling stage, at which time chromosome numbers were checked.

A total of 506 progeny were produced. Most of these plants (ca. 99%) had 21 or 22 chromosomes (Figures 2 and 3). The chromosome numbers of remaining exceptional progeny and the trisomic parent used to produce them were: two plants with 7 chromosomes from the cross involving Trisomic 7; one plant with 19 chromosomes (Figure 4) involving Trisomic 4; one with 20 chromosomes (Figure 5) involving Trisomic 3; two with 21 plus a telosome from Trisomics

<table>
<thead>
<tr>
<th>Trisomic type</th>
<th>Number of florets pollinated</th>
<th>Total no. of progeny obtained</th>
<th>Frequency and (%) of progeny with:</th>
<th>Expected trisomic transmission†</th>
<th>χ² value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>21 chromosomes</td>
<td>22 chromosomes</td>
<td>Others*</td>
</tr>
<tr>
<td>1</td>
<td>2,537</td>
<td>81</td>
<td>69(85.2)</td>
<td>11(13.6)</td>
<td>1(1.2)</td>
</tr>
<tr>
<td>2</td>
<td>2,843</td>
<td>57</td>
<td>55(96.5)</td>
<td>1(1.8)</td>
<td>1(1.8)</td>
</tr>
<tr>
<td>3</td>
<td>1,015</td>
<td>75</td>
<td>72(96.0)</td>
<td>2(2.7)</td>
<td>1(1.3)</td>
</tr>
<tr>
<td>4</td>
<td>975</td>
<td>39</td>
<td>28(71.8)</td>
<td>10(25.6)</td>
<td>1(2.6)</td>
</tr>
<tr>
<td>5</td>
<td>1,651</td>
<td>60</td>
<td>52(86.7)</td>
<td>8(13.3)</td>
<td>0(0.0)</td>
</tr>
<tr>
<td>6</td>
<td>2,283</td>
<td>99</td>
<td>80(83.0)</td>
<td>18(18.2)</td>
<td>1(1.0)</td>
</tr>
<tr>
<td>7</td>
<td>1,924</td>
<td>95</td>
<td>79(83.2)</td>
<td>14(14.7)</td>
<td>2(2.1)</td>
</tr>
<tr>
<td>Total</td>
<td>13,228</td>
<td>506</td>
<td>435(86.0)</td>
<td>64(12.6)</td>
<td>7(1.4)</td>
</tr>
</tbody>
</table>

* See the text for details.
† Trisomic transmission frequencies reported by Yu (1968).
** Indicating significance at 1% level.
Mitotic metaphase in interspecific hybrids produced between trisomics and monotelotrisomics of *H. vulgare* and tetraploid *H. bulbosum*. The hybrids with 21 (Figure 2), 22 (Figure 3), 19 (Figure 4) and 20 (Figure 5) chromosomes are from the crosses involving trisomics. Those with 21 plus a telosome (Figure 6), 22 (Figure 7), 22 plus a telosome (Figure 8) and 7 plus a telosome (Figure 9) are from the crosses involving monotelotrisomics.
1 and 2; and one with 42 chromosomes from crosses with Trisomic 6. One hybrid with 21 chromosomes from the cross using Trisomic 1 was found to have some tillers with the haploid chromosome number (7).

The frequencies of 22-chromosome hybrid progeny from crosses with each trisomic type and their expected frequency are presented in Table 1. The expected frequencies of the extra chromosome transmission for each trisomic were based on the frequency of trisomic progeny obtained from crosses with diploid barley using trisomic plants as the female parent (Yu 1968). The differences between the frequencies of 21- and 22-chromosome plants and the expected frequencies were examined by the \( \chi^2 \) test.

The results revealed that the observed frequencies of 22-chromosome hybrid progeny were similar to the expected frequencies of the extra chromosome transmission for chromosomes 1, 4, 5, 6 and 7. This indicates that changing the ratio from 1V:2B to 2V:2B for these particular chromosomes did not increase chromosome elimination and that there are no major controlling factors on these chromosomes. However, the frequencies of 22-chromosome hybrid progeny were much lower than expected from crosses involving trisomics for chromosomes 2 and 3 (\( \chi^2 = 10.73 \) and 11.44 respectively, with 1 degree of freedom). It would appear that chromosomes 2 and 3 contain major genetic factors which are critical to the chromosome balance and stability in the interspecific hybrids between \( H. \) vulgare and \( H. \) bulbosum. However, the critical 8-chromosome progenies expected subsequent to chromosome elimination (see Figure 1) have not been found from these particular crosses.

**Telo Trisomics**

The data on the florets pollinated and seedlings obtained from crosses with the various monotelotrisomic lines and tetraploid \( H. \) bulbosum are presented in Table 2. The percentage seed set ranged from 40\% to 60\%. Between 55\% and 76\% of caryopses contained developing embryos and the frequency of embryos

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Chromosome numbers, observed and expected, in progeny from crosses between monotelotrisomics of diploid ( H. ) vulgare and tetraploid ( H. ) bulbosum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monotelotrisomic type</td>
<td>Number of florets pollinated</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Telo 2L</td>
<td>3,322</td>
</tr>
<tr>
<td>Telo 2C</td>
<td>124</td>
</tr>
<tr>
<td>Telo 2D</td>
<td>703</td>
</tr>
<tr>
<td>Telo 3L</td>
<td>879</td>
</tr>
<tr>
<td>Total</td>
<td>5,628</td>
</tr>
</tbody>
</table>

† See the text for details.
‡ Estimated from the progeny of selfed monotelotrisomics (Ho and Kasha, unpublished).
*, ** Indicating significance at 5\% and 1\% levels respectively.
germinating ranged from 42% to 87%. Only 28% to 39% of the embryos reached the seedling stage.

A total of 340 progenies were obtained from these crosses (Table 2). Most of them (97%) were the expected 21 and 21 plus a telosome hybrids (Figure 6). Six 22-chromosome hybrids (Figure 7) were also found in the progenies of these crosses: three from the cross involving Telo 2L, and one each from Telo 2C, Telo 2D and Telo 3L. A 22 plus a telosome hybrid (Figure 8) was found from the cross with Telo 2D. From crosses with Telo 2C, one 7 plus a telosome progeny (Figure 9) was found. Two 21-chromosome hybrids from crosses with Telo 2L were found to have some tillers with 7 chromosomes.

The observed and expected frequencies of 21 plus a telosome hybrid progeny from crosses with each monotelotrisomic line are presented in Table 2. The expected frequencies of telosomic transmission were obtained by checking their frequency in progeny obtained by self-fertilization of each monotelotrisomic (Ho and KASHA, unpublished results).

The frequency of 21 plus telosome hybrid progeny was similar to the frequency of telosomic transmission for Telo 3L, indicating that there is no major factor for chromosome elimination in the long arm of chromosome 3.

The frequency of hybrid progeny with 21 plus a telosome from crosses with Telo 2L was quite high (12%), but still significantly lower than the expected frequency (32%, $x^2 = 14.02$ with 1 d.f.). This indicates that the long arm of chromosome 2 does contain factor(s) which have some effect on chromosome elimination. A similar frequency of 21 plus a telosome progeny was obtained for Telo 2D, although the $x^2$ value was not significant based on the small numbers of progeny.

In the progeny from Telo 2C, one plant with 7 chromosomes plus a telosome was found, presumably due to chromosome elimination. It would appear that this unidentified chromosome arm contains major genetic factor(s) which are critical to chromosome balance and stability in the hybrids. While the frequency of hybrid progeny with 21 plus a telosome was also lower than expected, the number of hybrid progenies studied from this cross was relatively small. Nevertheless, the only critical plant with 7 plus a telosome (see Figure 1) was observed in progeny from this cross, indicating that chromosome elimination had occurred and that the telosomic arm contains controlling factors.

**DISCUSSION**

The primary objective of this study was to determine whether individual chromosomes control the apparent genome balance in interspecific hybrids between *H. vulgare* and *H. bulbosum*. The results from the crosses between the primary trisomic stocks and tetraploid *H. bulbosum* reveal that an extra dose of vulgare chromosomes 1, 4, 5, 6 or 7 did not upset the relatively stable 1V : 2B genome balance characteristic for triploid hybrids. However, when an extra chromosome 2 or 3 was present the 22-chromosome hybrids were rare, indicating that *H. bulbosum* chromosomes were usually eliminated. These results support
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The hypothesis (Kasha, Kao and Reinbergs 1970) that specific chromosomes carry genetic factors which are critical to chromosome stability in interspecific hybrids between *H. vulgare* and *H. bulbosum*. Kasha, Kao and Reinbergs (1970) observed that the rare hybrids formed between the cross of tetraploid *H. vulgare* and tetraploid *H. bulbosum* contained 27 rather than 28 chromosomes. They hypothesized that these hybrids most likely arose from a 13-chromosome *H. vulgare* gamete and the 14-chromosome gamete from the pollen parent *H. bulbosum*, resulting in a stable 1V:2B balance for one specific chromosome. On this basis, it might seem surprising to find that both chromosomes 2 and 3 strongly influenced chromosome stability in our interspecific hybrids. However, the 27-chromosome hybrids were rare, as were the 22-chromosome hybrids from crosses with the primary trisomic stock of chromosomes 2 and 3. This indicates that exceptional progeny could occur. Barclay, Shepperd and Sparrow (1972) conducted similar independent and concurrent studies and also suggested that chromosomes 2 and 3 exhibited control over chromosome elimination.

Crosses with the available monotelotrisomic stocks for chromosomes 2 and 3 were conducted to substantiate the results from the primary trisomics and to locate more specifically the genetic factors involved. The long arm of chromosome 2 had a significant effect on chromosome elimination. *Telo 2C* and *Telo 2D* have not yet been identified with marker genes, but it is probable that they involve chromosome 2. Both definitely influenced the level of chromosome elimination, as did the parent from which they originated, a primary trisomic for chromosome 2. *Telo 2D* is most likely telosomic for 2L since it was similar to *Telo L2* in plant morphology and the level of chromosome elimination expressed. *Telo 2C* is probably trisomic for the short arm of chromosome 2. It differs in plant morphology from *Telo 2L* and *Telo 2D*, and observations on chromosome size in root-tip cells (Figure 9) indicate it is likely the short arm of chromosome 2. However, chromosome size measurements cannot provide conclusive identification because of the size similarity of chromosomes 1 to 4 in barley. Furthermore, the recent studies of Tuleen (1973) indicate that the identity of the chromosomes to which linkage groups 1 to 3 were assigned may be incorrect. Since the known telotrisomics have been identified by marker gene associations they are referred to by linkage associations in this paper.

The only telotrisomic stock available for chromosome 3, *Telo 3L*, did not influence the genome balance or chromosome elimination. Since the primary trisomic for chromosome 3 influenced chromosome elimination, one could predict that such genetic factor(s) are located in the short arm of chromosome 3.

The results from the crosses with the telotrisomic stocks lead one to suggest that at least two and probably three or more genes are involved in the control of selective elimination of the *H. bulbosum* chromosomes, since it is probable that they are distributed in both arms of chromosome 2, and the short arm of chromosome 3.

From the observations on genome balance (Kasha and Sadasiviah 1971) and present evidence of its genetic control by specific chromosomes, it is reasonable to assume that the factors causing the elimination of the bulbosum chromosomes
are located on the *H. vulgare* chromosomes. These factors are offset or balanced by factors on the *H. bulbosum* chromosomes which, when present in sufficient dosage, neutralize the effects of the vulgare factors or, perhaps "protect" the bulbosum chromosomes. The relatively stable triploid hybrids provide clear evidence of stabilizing factors on the *H. bulbosum* chromosomes. Further evidence comes from a study of chromosome stability in hybrid endosperm tissues where Subrahmanyam and Kasha (1973) found that a genome combination of 1V : 4B was more stable than 1V : 2B. In addition, they reported that increasing the dosage of vulgare genomes will speed up the elimination of bulbosum chromosomes.

Evidence for the presence of genes acting in opposition on chromosome behavior has been reported before. In wheat, homoeologous chromosome pairing is inhibited by the *Ph* gene on chromosome 5B but is promoted by genes located on 5B and possibly minor factors on other chromosomes (Riley and Chapman 1967). The dosages of chromosome arms 5B and 5B influence the degree of homoeologous chromosome pairing. This type of interaction is similar to that between the genetic factors on *H. vulgare* and *H. bulbosum* chromosome that determine chromosome stability in the interspecific hybrids.

Until we can be more specific, we shall refer to the factors on the vulgare chromosomes as "V" factors and those on the bulbosum chromosomes as "B" factors. While a one-genome dose of V factors is stronger than a one-genome dose of B factors, it does not always lead to the elimination of the bulbosum chromosomes. In the reciprocal crosses between *H. vulgare* (2X) and *H. bulbosum* (2X), Kasha (unpublished) found that 2.6% of the progeny plants were diploid hybrids while the other were haploids of *H. vulgare*. Similar results can be obtained from the reciprocal crosses of the tetraploid forms of these two species. In the present study, two doses of B factors were usually able to balance or neutralize the function of one dose of V factors. From the crosses with the primary trisomics, a total of 506 progeny plants were produced. Of these, 504 were hybrids and only two plants (0.4%) were haploid. This frequency of chromosome elimination from triploid hybrids assumes that these 506 progeny represent the possibility of elimination, even though they account for only 10.7% of the florets fertilized. Lange (1971) found one haploid from crosses between diploid *H. vulgare* and tetraploid *H. bulbosum* with a similar elimination frequency of 0.4%. If any of these haploids had been produced by parthenogenesis (an expected rare event), the percentage of chromosome elimination would be still smaller or perhaps negligible. Thus, in contrast to the elimination of *H. bulbosum* chromosomes in 97.4% of the diploid hybrids, chromosome elimination from triploid hybrids is very low indeed.

From the crosses reported in Table 1, it is possible to obtain a separate estimate of the magnitude of the effect of factors on chromosomes 2 and 3 of *H. vulgare*. In the cross with Trisomic 2, 55 hybrids with 21 chromosomes were produced. Based on the expected trisomic transmission frequency, 16 hybrids with 22 chromosomes should have been produced. The observed frequency of one represents only 6.3% of those expected, or a chromosome elimination magnitude of
93.7%. Similarly, the magnitude of elimination for chromosome-3 factors is estimated to be 89.1%. Such estimates are very rough but indicate that the factors on either chromosome 2 or 3 are usually sufficient to cause elimination of *H. bulbosum* chromosomes when the V:B genomes are in 1:1 ratio.

Many factors could influence the frequencies of progenies obtained. One obvious question is whether the trisomic plants used for chromosomes 2 and 3 had an abnormally low transmission of the extra chromosomes. Chromosome number of selfed progeny from these and the other trisomic plants were checked and their transmission frequencies were comparable to those reported by Yu (1968). Furthermore, the brief report of Barclay, Shepherd and Sparrow (1972) independently substantiates the finding that chromosomes 2 and 3 control the elimination of bulbosum chromosomes.

The various progenies with exceptional chromosome numbers (2n = 7, 19, 20, etc.), which totaled to 1% from primary and 3% from monotelotrisomic crosses, were not associated with any particular chromosome and do not appear to add information pertinent to the objectives of the study. Their origin was most likely through the chance functioning of an aneuploid gamete from one of the parents or due to the chance elimination of chromosomes non-critical to the control of stability. The quite extensive pairing between chromosomes of the parental species and the suppression of nucleolus organizer regions of *H. bulbosum* chromosomes in hybrids (Kasha and Sadasiviah 1971) renders cytological identification of specific chromosomes impossible in an exceptional progeny.

The occasional hybrid plant with some haploid vulgare sectors indicates that elimination may occur subsequent to shoot primordia initiation. This rare or slower elimination from shoots is more typical of the results reported in tobacco (Gupta and Gupta 1973). The occasional haploid vulgare tillers can arise from diploid as well as triploid hybrids (Kasha, unpublished observations). On the other hand, chromosome counts in root-tip cells of any one hybrid plant are consistent.

Understanding the mechanism of chromosome elimination would be most useful for the purpose of being able to control it and increase the frequency of haploids obtained. Subrahmanyan and Kasha (1973) have demonstrated that the mechanism of chromosome elimination in the interspecific hybrids of *H. vulgare* and *H. bulbosum* is a gradual and somewhat variable process. Various mechanisms have been hypothesized such as genic disharmony (Lange 1971) and differences in cell cycle times and phases between the two species (Gupta 1969, relative to Nicotiana species; Rao and Johnson (1972) relative to mammalian somatic cell hybrids; and Subrahmanyan and Kasha (1973 relative to Hordeum species).

Sager and Ramanis (1973) have suggested that a system similar to that of "modification and restriction" in bacteria could account for maternal inheritance of chloroplast genes following sexual fusion in *Chlamydomonas reinhardi*. The chloroplast genes from the female parent are preferentially maintained, whereas those from the male parent are lost even though cells of equal size fuse. Rare exceptions to this rule occur when chloroplast genes from the male parent are
transmitted. SAGER and RAMANIS (1973) have also suggested that chromosome loss following somatic fusion of mammalian cells might be due to a similar process. DAVIES (1974) has proposed that the same hypothesis might explain chromosome elimination in hybrids between *H. vulgare* and *H. bulbosum* and those between *Nicotiana tabacum* and *N. plumbaginifolia*.

Furthermore, DAVIES suggested the latter hypothesis may be open to test since SAGER and RAMANIS (1967, 1973) have shown that chemical and UV radiation treatments can influence the frequency of paternal transmission. PONTECORVO (1971) also observed that X-ray or gamma irradiation of one parent before somatic cell fusion of mouse and Chinese Hamster cell lines would predetermine which chromosomes were preferentially lost.

An additional area of interest in chromosome elimination is the preferential loss of a set of chromosomes from germ-cell nuclei in embryos of certain Diptera insects. BANTOCK (1970) has found polar granules which he hypothesized were responsible for preventing the loss of chromosomes. The assay and function of these granules would be of interest.

The applications of chromosome elimination mechanisms are of great interest. WEISS and GREEN (1967) have shown that the elimination of chromosomes in the hybrids between somatic cells of mouse and man is very useful for locating human genes to individual human chromosomes. KASHA and KAO (1970) have proposed that haploid vulgare plants produced by elimination of *H. bulbosum* chromosomes from the interspecific hybrids are of value in barley breeding programs. In the opposite direction, SAGER and RAMANIS (1973) have reported that the blocking of chloroplast DNA elimination mechanism by UV irradiation permits the production of large numbers of biparental zygotes for genetic analysis in Chlamydomonas.

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**LITERATURE CITED**


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