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# THE CONTROL OF DIPLOID-LIKE MEIOSIS IN POLYPLOID TAXA OF *CHRYSANTHEMUM* (COMPOSITAE)

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Twenty of the twenty six species and varieties of Japanese *Chrysanthemum* are either tetraploid, hexaploid, octoploid, or even decaploid on a basic haploid genome of nine chromosomes. Although the genomic constitution of these polyploids has not been established, the evidence of interspecific cross fertility as well as morphological and ecological evidence suggests that only two or three diploid species were involved in the establishment of the polyploid series (Shimotomai 1933). In hybrids between diploids nine bivalents are regularly formed (Tanaka 1959). In all the polyploids bivalent formation is the norm, and multivalents are rare; they may be autoploids with a genic mechanism for the stabilisation of pairing.

Precise genomic analysis requires artificial hybridization between the diploid and several polyploid levels. Diploid × tetraploid hybrids are easily obtained (Takemoto 1939; Tanaka 1952), but hybridization attempts between the diploids and the higher polyploids have almost invariably failed,—the $F_1$ embryos collapse during early development (Tanaka and Watanabe 1972). The barrier has been overcome by ovary culture on a modified Miller's artificial medium (Watanabe, in preparation), and meiotic studies of diploid × high polyploid hybrids have been achieved.

## MATERIALS AND METHODS

The following parental plants were collected from their native localities;
*Ch. boreale* Makino, (2n=18, 2x), Koyaguchi, Wakayama Pref.
*Ch. japonense* f. *debilis* Kitam., (2n=54, 6x), Saka, Hiroshima Pref.
*Ch. japonense* v. *octoploid*, (2n=72, 8x), Yakushima Isl., Kagoshima Pref.
*Ch. ornatum* Hemsl., (2n=72, 8x), Akune, Kagoshima Pref.
*Ch. japonense* v. *crassum* Kitam., (2n=89, 10x−1), Tokunoshima Isl., Okinawa Pref.
*Ch. pacificum* Nakal, (2n=90, 10x), Atami, Shizuoka Pref.

The methods of hybridization, ovary culture and mitotic examination will be reported fully in another paper (Watanabe, in preparation).

For meiotic analyses anthers were fixed 45% acetic acid and stained 1% aceto-orcein, applying the squash method.

## RESULTS

In Table 1 data are given on the frequencies of different chromosome associations in a number of species and species-hybrids. The table includes data from previous sources (Tanaka 1952, 1955; Shimotomai and Tanaka 1952; Kaneko 1961) as well as new data.

All six polyploid species (or varieties) form bivalents at a very high frequency. This frequency is 99.3% (1,430/1,440) of the possible in *Ch. pacificum*, 99.8% (1,668/1,672) in *Ch. japonense* v. *crassum*, 98.6% (2,166/2,196) in *Ch. japonense* v. *octoploid*, 95.5% (3,198/3,348) in *Ch. ornatum*, 99.1% (1,927/1,944) in *Ch. japanense* f. *debilis* and 96.8% (3,155/3,258) in *Ch. wakasaense*, respectively.

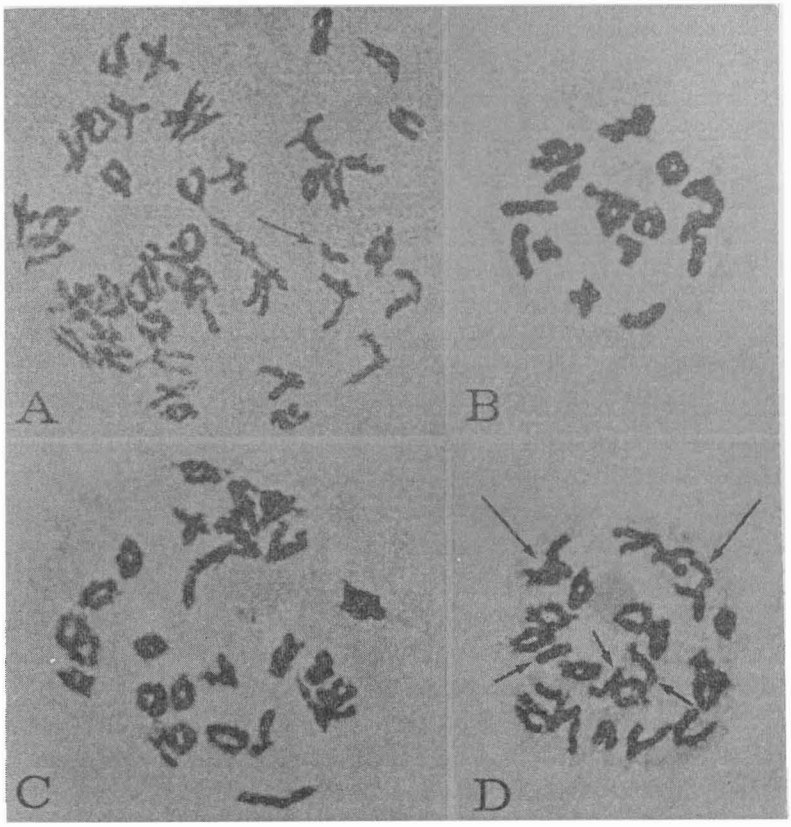


Fig. 1. Chromosome pairing in aneuploid *Ch. japonense* v. *crassum*, 2n=89 and in diploid × polyploid hybrids.
A, aneuploid 10x−1, 44 II+1 I (univalent, arrow);
B, *Ch. boreale*, 2x × *japonense* f. *debilis*, 6x, 18 II;
C, *Ch. boreale*, 2x × *japonense* v. *crassum*, 10x−1, 27 II;
D, *Ch. boreale*, 2x × *japonense* v. *octoploid*, 2 III+ 18 II+ 3 I. (trivalents; long arrow, univalents; short arrow) (×1,000).

Table 1. Meiotic chromosome pairing in polyploids and their hybrids of *Chrysanthemum*

| Plant | Somatic No. 2n | Mean pairing (Actual number of configurations) | | | | | | No. of cells |
|---|---|---|---|---|---|---|---|---|
| | | VI | V | IV | III | II | I | |
| *pacificum* | 90 (10x) | — | — | 0.16 ( 5) | — | 44.69 (1,430) | — | 32 |
| *japonense* v. *crassum* | 89 (10x−1) | — | — | 0.03 ( 1) | — | 43.89 (1,668) | 1.11 ( 42) | 38 |
| *japonense* v. *octoploid* | 72 ( 8x) | — | — | 0.23 ( 14) | — | 35.51 (2,166) | 0.07 ( 4) | 61 |
| *ornatum* | 72 ( 8x) | — | — | 0.72 ( 67) | — | 34.39 (3,198) | 0.34 ( 32) | 93 |
| *japonense* f. *debilis* | 54 ( 6x) | — | — | 0.10 ( 7) | — | 26.76 (1,927) | 0.08 ( 6) | 72 |
| *wakasaense** | 36 ( 4x) | — | — | 0.27 ( 48) | 0.01 ( 1) | 17.43 (3,155) | 0.06 ( 11) | 181 |
| *boreale* 4x × *pacificum*** | 63 ( 7x) | — | — | 1.33 ( 65) | 1.59 ( 18) | 24.76 (1,213) | 3.41 (167) | 49 |
| *okiense* 4x × *japonense* v. *crassum*** | 63 ( 7x) | — | 0.03 (1) | 0.17 ( 5) | 1.47 ( 44) | 26.40 ( 792) | 4.97 (149) | 30 |
| *boreale* 2x × *japonense* v. *crassum* | 54 ( 6x) | — | — | 0.28 ( 20) | 0.07 ( 5) | 26.11 (1,880) | 0.46 ( 33) | 72 |
| *okiense* 4x × *japonense* v. *octoploid*** | 54 ( 6x) | — | — | 0.16 ( 4) | — | 26.68 ( 667) | — | 25 |
| *okiense* 4x × *ornatum*** | 54 ( 6x) | — | — | 0.12 ( 3) | — | 26.48 ( 662) | 0.56 ( 14) | 25 |
| *boreale* 2x × *joponense* v. *octoploid* | 45 ( 5x) | — | — | 0.24 ( 14) | 0.60 ( 35) | 19.14 (1,110) | 3.95 (229) | 58 |
| *okiense* 4x × *japonense* f. *debilis*** | 45 ( 5x) | — | — | 2.65 (106) | — | 15.60 ( 624) | 5.85 (234) | 40 |
| *boleale* 2x × *japonense* f. *debilis* | 36 ( 4x) | — | — | 0.66 ( 76) | 0.03 ( 3) | 16.63 (1,912) | 0.03 ( 3) | 115 |
| *makinoi* 2x × *japonense* f. *debilis**** | 36 ( 4x) | — | — | — | 0.35 ( 11) | 16.16 ( 501) | 2.61 ( 81) | 31 |
| *wakasaense* × *makinoi** | 27 ( 3x) | — | — | — | 6.07 (510) | 2.93 ( 246) | 2.93 (246) | 84 |
| polyhaploid *indicum* 6x***** | 27 ( 3x) | 0.11 (10) | — | 0.05 ( 5) | 6.67 (614) | 2.05 ( 189) | 2.00 (184) | 92 |

* Data from Tanaka 1952, ** Kaneko 1961, *** Shimotomai and Tanaka 1962, **** Tanaka 1955.

The regularity of chromosome pairing in the hypo-decaploid *Ch. japonense* v. *crassum* and in the hybrids is illustrated in Fig. 1 A to 1 D. In the hybrids, ring bivalents are frequent, indicating the formation of at least two chiasmata in these.

In the hybrids between the diploid *Ch. boreale* and the hexaplaid *Ch. japonense* f. *debilis*, the octoploid *Ch. japonense* v. *octoploid* and the hypo-decaploid *Ch. japonense* v. *crassum* bivalent formation is also highly regular. This frequency is 92.4% (1,912/2,070) of the possible in 4x hybrid, 106.3% (1,110/1,044) in 5x hybrid and 96.7% (1,880/1,944) in 6x hybrid, respectively. There must be pairing between homeologues from different base sets derived from the polyploid parent. It must be inferred that the restriction on multivalent association in the polyploid species is not due to non-homology between corresponding chromosomes of the several basic sets. Rather, genetic control must be involved. Similar conclusions are to be drawn from the data quoted from previous sources.

It should be noted that in all hybrids there is a small but meaningful frequency of multivalents. The restriction of multivalents is a little less efficient in the hybrids than in the pure species.

The odd numbered hybrids (3x, 5x, 7x) provide, additionally, two kinds of information. First, the breakdown of control is much more severe at the 3x level, and less so at the higher levels. In fact, at the 3x level the frequency of trivalents was more than 70% of the possible. Secondly, the data on the 5x hybrid between *Ch.*

Table 2. Meiotic chromosome pairing in the hybrid (2n=45, 5x) *Ch. boreale* and *Ch. japonense* v. *octoploid*

| Pairing | No. of cells |
|---|---|
| 1 IV+2 III+14 II+7 I | 1 |
| 1 IV+1 III+18 II+2 I | 2 |
| 1 IV+1 III+17 II+4 I | 1 |
| 1 IV +19 II+3 I | 5 |
| 1 IV +18 II+5 I | 3 |
| 1 IV +17 II+7 I | 2 |
| 5 III+12 II+6 I | 1 |
| 3 III+17 II+2 I | 1* |
| 3 III+16 II+4 I | 1* |
| 2 III+18 II+3 I | 2* |
| 2 III+17 II+5 I | 4* |
| 1 III+20 II+2 I | 2* |
| 1 III+19 II+4 I | 5* |
| 21 II+3 I | 20* |
| 20 II+5 I | 5* |
| 19 II+7 I | 2* |
| 18 II+9 I | 1 |
| Total | 58 |

* Require small but significant amount of non-homologous intra-set pairings.

*boreale* 2x and *Ch. japonense* v. *octoploid* show that there must be a small but significant frequency of non-homologous association as distinct from homologous one, since the number of bivalents scored exceeds that possible on the null hypothesis that non-homologous associations can not occur. This fact is brought out more forcibly in the data of Table 2, which presents a breakdown of the frequencies of bivalent and multivalent associations. In no less than 42 out of 58 cells there must be some non-homologous pairs. It seems necessary to conclude that there must be limited segmental homology perhaps due to interchange, between essentially non-homologous members of the four basic sets of the octoploid. This view is supported by the occurrence of a low frequency of hexavalent and quadrivalent in the triploid polyhaploid *Ch. indicum* v. *hexaploid* (Tanaka 1955).

## DISCUSSION

The establishment of sexually self maintaining polyploid species or populations must require, generally, stable essentially diploid meiotic processes.

Several strategies are available whereby meiosis may be stabilised. One of these is true diploidisation, where the several genomes are either initially (as in a strict alloploid amphidiploid) or become by selection so different that association between them is not possible. Secondly, chiasma frequency might be strictly canalised at one chiasma per chromosome pair (Gupta and Koak 1976). Both of these strategies are negatived by the data presented here. Thirdly, there may be either spatial separation of the genomes during meiotic prophase, or there may be differences in condensation cycle such as is found in hybrids between *Brachycome lineariloba* and *B. campylocarpa* (Watanabe *et al.* 1976). The evidence in *Chrysanthemum* does not suggest these possibilities. Fourthly, there may be a degree of preferential association, perhaps based on slight structural differences between homoeologous. This appears to be the case in the classical *Primula floribunda* × *verticellata* hybrid. In the amphihaploid, bivalent formation is regular, although the chiasma frequency is reduced as compared with the pure species. In the amphidiploid, *P. kewensis*, there is also regular bivalent formation (Upcott 1939). *P. kewensis* is sexually fertile. Fifthly, there is the much more precise method of genic control, such as occurs in wheat (Riley and Chapman 1958, Sears and Okamoto 1958), where a single gene on chromosome 5B prevents homoeologous pairing. Similar control has been shown to occur in hexaploid oats (Rajhathy and Thomas 1961) and in tetraploid cotton and tobacco (Kimber 1961). Such control, if established by selection in a polyploid, would probably be based on a single gene on one genome only.

In *Triticum* and the other genera mentioned the "5B" gene is effective in either heterozygous or hemizygous dosage. However, in the hexaploid *Festuca arundinacea* Jauhar (1975) has argued for the existence of a similar system ineffective in the hemizygous state.

In the Japanese polyploid taxa of *Chrysanthemum* only the strategies of preferential pairing or of a 5B type gene ineffective in the amphihaploid condition are possible.

But further precise genomic analyses to clarify the degree of differentiation between the several genomes in polyploids and the monosomic or nullisomic analyses must be required to prove which strategy is available for these perennial polyploid taxa of *Chrysanthemum*.

It might be possible only in perennials not in annuals required rapid meiotic stabilisation that the gradual divergence of homoeologues by the selective accumulation of many small changes of chromosome structure leads to the establishment of diploid like meiosis, the preferential pairing in polyploids.

In the evolution of the diploidisation mechanism it seems possible that a limited degree of preferential pairing in a polyploid could lead to the selection of a gene or gene complex in one of the basic genomes to give more efficient control of pairing, and increased fertility. Initially weak, such a gene might be ineffective or insufficient in single dosage in the amphihaploid or hemizygous state. It could only be selected for in polyploids, not in diploids.

## SUMMARY

Genetic stabilisation of diploid-like meiosis occurs in hexaploid, octoploid and decaploid taxa of *Chrysanthemum*. This stabilisation is ineffective in $F_1$-hybrids between diploids and the several polyploids which have been obtained by ovary culture. The suppression of multivalent formation is effective in even-ploid hybrids although they are amphihaploid. A significant frequency of trivalents occurs in odd-ploid hybrids.

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