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Studies on the control of diploid-like meiosis in polyploid taxa of *Chrysanthemum*

4. Colchiploids and the process of cytogenetical diploidization

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Summary. Chromosome pairing during meiosis was studied in colchiploids of *Ch. japonense* 6X and *Ch. boreale* 2X. In both species chromosomes paired predominantly as bivalents, even though because of complete homology they possess the ability to pair as multivalents. Multivalent formation is prevented by restriction of pairing initiation to a single site (=zygomere) per chromosome. Multivalent suppressor systems in polyploids may evolve through gradual reduction in number of zygomeres, and differentiation in their homology recognition and regulation system.

Key words: Diploidization – Zygomere reduction – Colchiploid – Meiosis – *Chrysanthemum*

Introduction

In the native Japanese species of *Chrysanthemum* (=*Dendranthema* Kitamura 1978), polyploidy has played an important role in evolution, and has given rise to tetraploids, hexaploids, octoploids, and decaploids. In all polyploid pure species and in all even-numbered polyploid hybrids except *Ch. yoshinaganthum* (Tanaka 1960), bivalent formation is the norm, and multivalents are rare. On the other hand, in odd-numbered polyploids, especially in triploids there is extensive multivalent formation as well as intragenomic pairing. Extensive homoeologous bivalent pairing without differential affinity has been revealed in the depolyploidized derivatives of polyploid species successively crossed with a single diploid species. The chromosomes of even-numbered polyploids thus pair with each other as obligate bivalents in spite of complete or almost complete pairing affinity between different genomes (Watanabe 1977, 1981 a, b, c).

For an explanation of the obligate bivalent formation in even-numbered *Chrysanthemum* polyploids, the following hypothesis was proposed;

1. Chromosome pairing can be initiated at two sites A and B. The two sites are under independent and fundamentally different genic control.
2. At either site pairing is always two-by-two, the strands involved at the A site being independent of those involved at the B site.
3. The initiation of pairing at the A site always precedes that at the B site.
4. The initiation of pairing at the B site can be suppressed by polygenic control.

Multivalent suppressor systems work very well in even-numbered polyploids of *Chrysanthemum* but does not work well in most triploids for reasons which are not understood.

One critical test of this hypothesized mechanism of a multivalent suppressor system would be the study of meiosis in induced colchiploids of polyploid chrysanthemums. If the absence or rarity of multivalents is confirmed during meiosis, this would then support the hypothesis that a genetical control as mentioned above operates in cytological diploidization of the colchiploid and the corresponding polyploid species.

The purpose of this article is to examine the pairing behaviour of the colchiploids, and to discuss the evolution of multivalent suppressor systems in polyploids.

Materials and methods

Hexaploid (2n=6X=54) *Ch. japonense* Nakai (Uchinoura Strain) and diploid (2n=2X=18) *Ch. boreale* Makino (Hanaizumi Strain) were used. Achenes of these species were kindly provided by Professor Dr. R. Tanaka (Laboratory of Plant Chromosome and Gene Stock, Hiroshima University, Japan).

Cotton plugs immersed in 0.4% aqueous colchicine were put on the emerging apical tips between the two cotyledon leaves. The seedling were subjected to such treatments for three days of 4 h duration each day. Affected plants were initially slow growing with thicker and variously deformed leaves.

Results and discussion

Each colchiploid derived from *Ch. japonense* 6X and *Ch. boreale* 2X was examined. These colchiploids had thicker stems, leaves and involucural bracts, and slightly larger flowers than the corresponding untreated plants.

Figure 1 is a metaphase I spread from the colchiploid (12X) of *Ch. japonense* 6X. The meiotic analyses are summarised in Tables 1 and 2. Meiosis was remarkably regular, the number of mutivalents being low and the number of bivalents high. The general range was 0–2 quadrivalents per cell with an average of 0.35 in the colchiploid (12X) of *Ch. japonense,* and was 0–4 quadrivalents per cell with an average of 1.29 in the colchiploid (4X) of *Ch. boreale.* Moreover, in about 68% of PMCs of the former, as opposed to only 26% of PMCs of the latter, there was no multivalent association. Trivalents were rare and were probably the result of disjoined quadrivalents. Any higher association than quadrivalent was absent.

The data of quadrivalent frequency in the colchiploid (4X) of *Ch. boreale* conform to the theoretical Poisson expectation based on a hypothesis of randomness ($\chi^2 = 5.2554$, d.f. = 4, $0.20 < P < 0.30$). All sets of four chromosomes therefore have an equal chance of forming a quadrivalent. In previous papers (Watanabe 1981 a, b, c), *Ch. boreale* (2X) chromosomes were suspected of having two active zygomeres per chromosome. However, the quadrivalent frequency here in the tetraploid is considerably below the expected value of ⅔ for two active zygomeres per chromosome (Sved 1966). Therefore there must be some control which leads to predominant bivalent formation at the tetraploid level, even though the chromosomes are fully homologous. Incomplete zygomere localization must therefore have already been attained at the diploid level. The frequency of quadrivalent formation in the colchi-

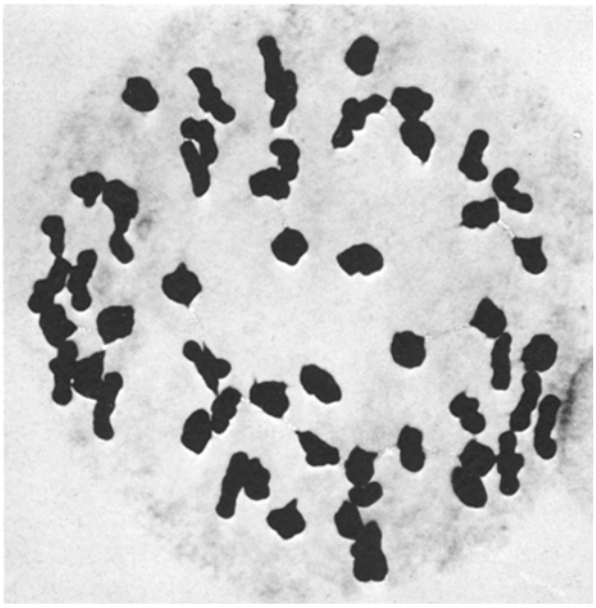

Fig. 1. Metaphase I configuration in a colchiploid of *Chrysanthemum japonense* 6X, showing 53 II + 2 I (X1500)

Table 1. Meiotic chromosome configurations in the colchiploid (12x) of *Ch. japonense* (2n = 6x = 54). Mean: (0.35 ± 0.12) IV + (0.06 ± 0.04) III + (51.97 ± 0.30) II + (2.45 ± 0.35) I. The frequency of bivalent formation is 96.2%

Configurations	No. PMC
2 IV + 49 II + 2 I	2
2 IV + 48 II + 4 I	1
1 IV + 52 II	1
1 IV + 51 II + 2 I	2
1 IV + 50 II + 4 I	2
1 III + 51 II + 3 I	2
54 II	8
53 II + 2 I	4
52 II + 4 I	6
51 II + 6 I	3
Total nos of PMC	31

Table 2. Meiotic chromosome configurations in the colchiploid (4x) of *Ch. boreale* (2n = 2x = 18). Mean: (1.29 ± 0.10) IV + (0.03 ± 0.02) III + (15.14 ± 0.20) II + (0.47 ± 0.10) I. The frequency of bivalent formation is 84.1%

Configurations	No. PMC
4 IV + 10 II	2
3 IV + 12 II	14
3 IV + 11 II + 2 I	3
2 IV + 1 III + 12 II + 1 I	1
2 IV + 14 II	24
1 IV + 1 III + 14 II + 1 I	3
1 IV + 16 II	29
1 IV + 15 II + 2 I	9
1 IV + 14 II + 4 I	1
1 IV + 13 II + 6 I	1
18 II	25
17 II + 2 I	4
16 II + 4 I	1
15 II + 6 I	1
Total nos of PMC	118

ploid *Ch. japonense* 12X is significantly lower than in that of the colchiploid *Ch. boreale* 4X. The multivalent suppressor system in the former parental species has therefore become more consolidated than in the latter one.

All these data are consistent with the presence of a genetic multivalent suppressor system in *Chrysanthemum*.

Quadrivalent frequency lower than the expected have previously been found, and have been explained in terms of preferential pairing based on the heterozygous nature of the materials investigated (Swaminathan and Sulba 1959; Venkateswarlu and Rao 1963; Arora 1975; Madhusoodanan and Arora 1979). Most of these reports, however, lack the genetic evidence of disomic inheritance that would support this speculation. Additionally, chromosomal rearrangements with breakpoints clearly outside regions of pairing initiation do not induce preferential pairing (Walters and Gerstel 1948; Linnert 1962; Sybenga 1965, 1966a, b, 1970).

In the model proposed previously (Sybenga 1966c, 1969; Watanabe 1981a, b, c) and discussed here, the extent of pairing between related chromosomes depends on zygomere number and homology and on the nature of the pairing regulation system, not on the heterogeneity of the structural genes throughout the whole chromosome. Consequently, the degree of bivalent formation is not necessarily consistent with the degree of genic diploidization. This is particularly clear in the case of the 4X colchiploids, in which the low amount of quadrivalent formation can not be explained in terms of reduced homology in the diploid. In addition, the equal probability of quadrivalent formation for each of the chromosome sets argues in favour of an overall control mechanism rather than a mechanism which depends on the independent divergence for each chromosome set.

The following proposes a sequence for the evolution of a multivalent suppressor system, and examples are given (Fig. 2). It is assumed that polyploids with disomic genetical behaviour are at an advantage over those with multisomic behaviour, because of the regularity of meiosis, the advantage of fixed heterozygosity, and the stabilization of the genome. Therefore selection will in general favour change leading from multivalent formation and multisomic inheritance to bivalent formation and disomic inheritance.

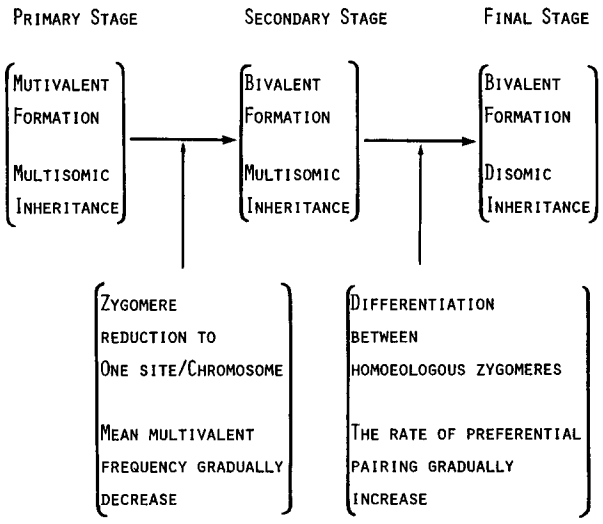

Fig. 2. Process of cytogenetical diploidization

The evolution of a multivalent suppressor system is ultimately an adaptive process that involves intrinsic barriers to chromosome replacement between originally homologous chromosomes, by the improvements of the recognition system through the reduction of pairing initiation to a single site per chromosome, and the differentiation of zygomere DNA base sequence and their regulation system. Although three stages are tentatively distinguished, the shift from one stage to another seems to be a gradual process. Consequently, there are numerous conditions intermediate between these three stages.

Primary stage

In this stage more than two zygomeres per chromosome at sufficient distance from each other are usually active in the same pairing period. All homologous or homoeologous chromosomes of each set show random association, leading to multivalent formation. There is a free choice of pairing partner. This implies that at anaphase I, when half the chromosomes of each set of homologues or homoeologues move to each pole, these halves constitute a random sample from the originals, which is the basis of multisomic inheritance. Multivalent formation frequently introduces the risk of unequal separation, leading to sterility. Natural polyploids at the Primary stage may reduce this risk by vegetative (in *Chrysanthemum yoshinaganthum,* Tanaka 1960; in *Lilium tigrinum,* Noda 1974) or apomictic reproduction (in polyploid *Eupatorium chinense* var. *simplicifolium,* Watanabe et al. 1982), or cytogenetical diploidization leading to the Secondary and Final stages.

Intermediate stage

The shift from Primary to Secondary stage seems to occur gradually, and to affect the entire genome, as suggested in colchiploid *Ch. boreale* and other hybrid derivatives (Watanabe 1981a, b, c). The distribution of quadrivalent follows the Poisson or binomial expansion in these tetraploids although the mean quadrivalent frequency is different in each genetic strain.

Similar random distribution of quadrivalents has been obtained in *Dactylis* tetraploids (McCollum 1958). Mutations which lead to zygomere localization may be masked at the diploid level, except for asynaptic mutants in which pairing is

totally suppressed. However such variation in this genetic system among strains of the same species can be revealed under competitive conditions, such as in the induced 4n *Lycopersicum esculentum*, 4n *Asparagas officinalis*, 4n *Oriza sativa* and 4n *Secale cereale* (Gottschalk 1978). There are great differences with regard to the quadrivalent frequency among colchiploids in these species. Exclusively bivalent fromation was also found in induced autotetraploids of *Datura suaveolens* (Goodspeed and Avery 1929), *Solanum rybinii* (Rybin 1940), *Agathae coelestris* (Reese 1956), *Tagetes erecta* (Bolz 1961) and *Zinnia linearis* (Bose and Panigrahi 1969). These strains of each species may be regarded as ready to attain the Secondary stage in respect of the multivalent suppressor system.

Secondary stage

In this stage a single zygomere per chromosome is usually active, and only bivalents are formed. All homologous or homoeologous chromosomes in each chromosome type may replace each other. Thus the genetic behaviour remains basically multisomic, namely tetrasomic inheritance in tetraploid and hexasomic in hexaploid. Although zygomeric activity is restricted to one site per chromosome, the differentiation of zygomere DNA base sequences in each chromosome type is not sufficient to limit exchange between homoeologues. Japanese polyploid chrysanthemums, with the exception of *Ch. yoshinaganthum*, seem to be at this stage.

The cytogenetical conditions in *Chrysanthemum* are paralleled to a large extent by similar phenomena in *Phleum pratense* (Müntzing and Prakken 1940), *Lotus corniculatus* (Dawson 1941), *Solanum nigrum* (Jørgensen 1928), *S. tuberosum* (Lunden 1937; Lamm 1938, 1945), polyploid *Fragaria* (Lilienfeld 1933), and *Fragaria* × *ananassa* (Byrne and Jelenkovic 1976).

Unfortunately, distinct segregation ratios have not yet been obtained in polyploid chrysanthemums, but the hexasomic inheritance in *Phleum pratense* (2n = 6X = 42, Nordenskiöld 1953, 1957) and the tetrasomic inheritance in *Lotus corniculatus* (2n = 4X = 24, Dawson 1941) and *Tulipa chrysantha* (2n = 4X = 48, Darlington and Mather 1949) are matched with obligate bivalent formation during meiosis.

To fix mutations in the Primary and Secondary stage, many more generations are required than in the Final stage; multisomic inheritance in the Primary and Secondary stages implies a buffering system against the fixation of mutated genes.

Intermediate stage

The shift from the Secondary stage to the Final stage seems to proceed gradually and independently on each set of chromosomes. This process seems to be a gradual differentiation of the DNA base sequence of zygomeres (recognition sites or protein binding sites) between homologous and homoeologous zygomeres. In this Intermediate stage homologous pairs form preferentially, but occasional homoeologous pairing also occurs between the similar but not homologous chromosome of the polyploid set. This situation has been observed in the polyploid fern *Ceratopteris* (Hickok 1978).

Final stage

In this stage, a single zygomere per chromosome is usually active, and the differentiation of zygomeric DNA in each chromosome type is sufficient to limit exchange between homoeologues. There is no free choice of partner. Homoeologous chromosomes do not pair, even when they are nearly identical in structural genes. Only bivalents can be formed, always involving the same partners. The genetic system is disomic. Tetraploid and hexaploid wheat and tall fescue (Malik and Tripathi 1970; Jauhar 1975 a, b; Lewis et al. 1980) seem to be in this stage.

If the multivalent suppressor gene or gene complex is deleted in these plants, pairing between homoeologous chromosomes will again be possible and multivalents will be observed in meiosis (Okamoto 1957; Sears and Okamoto 1958; Riley and Chapman 1958; Jauhar 1975 a).

It has been found that in wheat-rye hybrids lacking the wheat 5B chromosome, pairing between homoeologous chromosomes within the wheat genome is below the expected level (Riley and Law 1965). The rye genome can partly take over the function of suppression of zygomere activity exerted by the 5B chromosome of wheat. Homoeologous pairing in nulli-5B of wheat must be induced by the neozygomeres which retain a considerable degree of homology between homoeologues. The activity of these neozygomeres is however suppressed by the *Ph* gene under normal conditions. The functioning zygomeres, on the other hand, are unaffected by *Ph*, but lack the homology to be capable of pairing between homoeologues. Thus one of the actions of *Ph* gene in wheat might be to suppress the zygomere activity of some latent zygomeres and lead to the zygomere reduction to a single site per chromosome, in addition to the regulation of spatial arrangement of chromosomes in somatic and premeiotic cells as suggested by Feldman (1966), Feldman et al. (1966) and Feldman and Avivi (1973). Originally, the multivalent suppressor system seems to have been under polygenic control in wheat, too. One (5B-gene) of these suppressor genes might have dominated over or even have suppressed another 3D-gene (Mello-Sampayo 1968, 1971; Upadhya and Swaminathan 1967), 3A-gene (Drisioll 1972) and others by mutation.

Such single gene control systems are not known in many other allopolyploids, but there is no doubt that genetic regulation of chromosome association, restricting pairing between homoeologous chromosomes without appreciably impairing association between homologues, is a general phenomenon in well established allo-

polyploids. The consolidation of a multivalent suppressor system may occur more quickly in annuals without vegetative or agamospermous reproduction than in perennial herbs, shrubs and trees.

Due to the zygomere reduction, certain aberrations may not be discovered cytologically, and some will not reduce fertility. Recombination in the segments involved is inhibited and the segments are transmitted as gene-blocks. The fewer zygomeres there are, the greater the number and size of cryptic aberrations possible, the quicker the fixation of mutated genes will occur than at the Primary and Secondary stage. A combined process of mutation, deletion and rearrangements may gradually reduce and eventually eliminate the duplicated genes of homoeologues, leading to the true differentiation between homologues and homoeologues.

In *Zea* and *Lilium,* pairing may be initiated at many sites along the chromosomes (Burnham et al. 1972; Holm 1977). Here, rearrangements with interstitial breaks involving zygomere(s) are able to induce preferential pairing and a high frequency of multivalent formation in the polyploids (Gilles and Randolph 1951; Morrison and Rajhathy 1960; Shaver 1962; Doyle 1963; Noda 1974). These are difficult to diploidize and stabilize in the polyploid condition. This might be one of the major reasons why polyploidy does not play an important role in the evolution of this genus.

It should be possible to produce stable breeding strains with still higher chromosome multiples when we use the materials involving low numbers of zygomeres.

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