Preferential Chromosomal Transmission in *Matricaria chamomilla* L. Aneuploids

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The progeny of colchiploids may be heterogenous, unless and until certain mechanisms like acute preferential pairing leading to exclusive bivalent formation or perfect disjunction of quadrivalents are in operation. In the absence of such systems, unequal disjunction of multivalents in autotetraploids gives rise to gametes with deviant chromosome numbers which if not eliminated in preference to normal ones, on fertilization, result in different chromosomal types. The colchiploid of common 'Blue Oil' plant *Matricaria chamomilla* falls in the latter category where, in the absence of perfect disjunction of quadrivalents, different chromosomal types originate with each one having the potentiality of forming different polysomics.

Material and methods

Seeds collected from raw autotetraploid of *M. chamomilla* L. were sown in a pan. Twenty five seedlings were transplanted in pots and were grown under identical conditions. Root tips, after 2 hours pretreatment with PDB, were fixed in acetic alcohol (1:3). The material was kept for 24 hours in the fixative and was squashed in 1% aceto-orcein solution. For meiotic studies young inflorescences were fixed in Carnoy's fluid to which little ferric acetate was added. Estimate of pollen fertility is based on its stainability in aceto-carmine.

Observations

Origin of polysomic types

Fig. 1 depicts the frequency of various chromosomal types of *M. chamomilla* obtained from a hypotetraploid plant with 2n=35 (4x-1) which was originated from an induced autoploid (2n=36). Phenotypically, the different chromosomal types could not be distinguished each other and also from the parental type at the seedling stage. Compared to the progenitor, their growth was slow and, in general, the mature plants were dwarf, compact with thicker stem and leaves. The flowering was also delayed in all of them as compared to the raw tetraploid. Except the plants with 2n=36 (obtained in the progeny) all the chromosomal forms bore very few capitula.

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Chromosomal identification

The eighteen somatic chromosomes of diploid *M. chamomilla* fall in 2V+5L+2J wherein subterminal chromosomes (J) are smallest in the complement (Fig. 2a). The progenitor of the present chromosomal types has each chromosome represented in fours, except one median chromosome of the IVth quadriplex. Fig. 2b represents the somatic chromosomes of plant with 2n=33 wherein 3 median chromosomes of the IVth quadriplex were lacking, otherwise all the chromosomes were exactly represented four times. Plant with 2n=34 shows the absence of one median in the IVth and a submedian in the Vth quadriplex (Fig. 2c). Out of 7 plants with 2n=35, one had 9 subterminal chromosomes (Fig. 2e) instead of the normal eight and Vth and VIIth sets in the complement were represented by three chromosomes each. The rest of the plants with 2n=35 (Fig. 2d) has all but one submedian chromosome of Vth set. The two hypertetraploids (2n=37) also differed karyotypically. One of the plants had an extra submedian chromosome in the 1st quadriplex in addition to the normal 9 sets of four (Fig. 2f). The other plant was conspicuous in as much as the chromosomes in the 1st, Vth and VIth sets were in three; VIIth set was represented by two and IVth and VIIIth sets were hexaplex. Furthermore, the two submedian chromosomes were new as apparent by size and were not analogous to any of the nine basic sets in the complement (Fig. 2g).

Meiosis

Meiotic data of different types, i.e., 2n=33, 35, 36 and 37 are summarised in the Table 1. Chromosomal associations upto quadrivalents were discernible in all of them (Figs. 3–5), while in one of the plants with 2n=35 few pentavalents were also observed. At anaphase I, even though the chromosome disjunction was almost regular, occurrence of unequal segregation, late disjunction and laggards were not rare. The percentage of pollen fertility ranged from 18.54 (2n=37) to 70.24 (2n=36) (Table 1).
Buds collected from the plant with 2n=33 when grown at an atmospheric temperature of ca. 41°C showed almost total desynapsis. Diakinesis and metaphase I was conspicuous in having poor spindle and displaying complete absence of quadri-
Discussion

The raw colchiploid of *M. chamomilla* raised earlier (Madhusoodanan and Arora 1979) does not breed true with respect to its chromosome number because of irregular disjunction of multivalents and unequal segregation of univalents en-

Figs. 3–8. Normal meiosis. 3–4, diskinesis, 2 IV+2 III+9 II+1 I (2n=33) and 3 IV+11 II+1 I (2n=35). 5, metaphase I, 2 IV+12 II+5 I (2n=37). 6–8. Desynaptic meiosis. 6, diakinesis, 4 II+25 I (2n=33). 7, metaphase I, 2 II+29 I (2n=33). 8, anaphase separation resulting in a polyad (2n=33). All ca. ×1250.
suing in aneuploid gametes which are not weeded out during gametic and/or zygotic selection. Moreover, vegetative propagation of the plant is not possible. Though 90% of its progeny were tetraploids, two aneuploid types (2n=35 and 37) were also obtained which had fairly good fertility (Madhusoodanan and Arora 1978). In the succeeding generation of the hypotetraploid (2n=35), the unequal segregation of chromosomes at anaphase I (18/17, 16/19 and 15/20) resulted in a range of chromosomal types. As is apparent from the histogram (Fig. 1), the sex cells with less than 16 chromosomes seem to be incapable of fertilization since no chromosomal type below 2n=33 was obtained. Out of 25 plants screened, 36% were tetraploid which were similar to its counterpart in all morphological features. However, they showed an average of 13.33 bivalents and 1.05 univalents per cell as compared to 12.68 and 1.45 observed in raw colchiploid.

Karyological analyses of different polysomics reveal an explicit trend in the elimination and/or selecton of the chromosomes, which is not random. Smallacrocentric chromosomes seem to confer a selective advantage while, generally median/submedian chromosomes are eliminated in most of the cases. Darlington and Mather (1944) have shown that in triploid Hyacinthus the chances of chromosome being lost is greatest for small ones wherein chance of effective pairing and chiasmata formation is less. However, the present case does not hold true for such a surmise, as the centromere position and not the size of chromosome is responsible for its transmission to the succeeding progeny where the gain is constantly confined to the smaller subterminal chromosomes and the loss is not for the larger submedian chromosomes. The gain of only smaller chromosomes in the complement in unstable hybrid clone is also reported in Amaryllis (Khoshoo and Narain 1967). In the present case preferential transmission of small subterminal chromosomes in their complement, indicating probably their indispensability for a viable gamete. Furthermore, origin of hypotetraploid with additional subterminal (Fig. 2e) also point towards the preferential selection for such chromosomes though only one such plant was obtained in the small progeny which was scrutinised cytologically.

The hypertetraploid (2n=37) with an aberrant karyotype (Fig. 2g) having 10 subterminal chromosomes in the complement and a heteromorphic pair (large and small submedian chromosomes) appears to represent the product of an interchange translocation. Its meiotic analysis reveals preponderance of bivalents (13.35 per cell), low number of quadrivalents (1.67 per cell), and the unequal segregation results in 18.54% pollen stainability.

Raw colchiploid (2n=36) had 1.85 quadrivalents per cell (Madhusoodanan and Arora 1979) but the plant with 2n=33, obtained from the hypotetraploid, displays an increased quadrivalent frequency (2.17 per cell). The plant is karyotypically similar to the tetraploid except that it lacks 3 median chromosomes of the IVth quadrilplex. Theoretically one would expect lower multivalent frequency in hypotetraploids but the higher frequency in this particular case seems to indicate a positive correlation between multivalent formation and absence of the metacentric chromosomes. However, detailed meiotic analysis of the various other hypotetraploids, which at present is inadequate, only can clarify this point.

The total absence of multivalents and the occurrence of only low frequency of
bivalents at metaphase I (2.80 per cell) in the plant with 2n=33 when the flower buds were collected at 41°C definitely indicates effect of temperature on pairing behaviour of chromosomes of the plant which had otherwise normal meiotic process. The temperature induced desynapsis is reported in a number of plants including the staple food crops like rye (Prakken 1943); wheat (Li et al. 1945) and rice (Wang et al. 1965). It is believed that desynapsis involve changes in the chemical structure and Ito et al. (1967) have shown that the inhibitors of protein on RNA synthesis have to be effective at all meiotic stages upto and including part of diakinesis in preventing chromosome pairing. In the present case high temperature had affected the meiotic behaviour of the particular plant and not the other aneuploids grown under identical condition which exhibited normal pairing. This implies that the process of desynapsis has been accentuated by the loss of three homologous chromosomes of the IVth set of its complement.

Summary

Various chromosomal types were obtained from a hypotetraploid (2n=35) of M. chamomilla L. isolated from the progeny of an induced autotetraploid plant. Karyological analysis reveals preferential transmission of small subterminal chromosomes as these are never eliminated in any of the aneuploids obtained. The absence of 3 median chromosomes from the fourth quadruplex of the plant with 2n=33 seems to boost multivalent frequency and also accentuates desynapsis caused by high temperature.

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