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CYTOGENETICAL EVOLUTION OF GARDEN CHRYSANTHEMUM

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ABSTRACT

Garden chrysanthemum (*C. morifolium* Ramat.) is a polyan euploid complex ($2n = 36, 45, 47, 51-75$) and 183 cultivars grown in India have been analysed with a view to obtaining an idea about the underlying mechanisms of the genetic-evolutionary differentiation. It has originated in China but considerable evolution, under the direction of man, took place in Japan and various gardens of the world. There is no correlation between the grade of ploidy and capitulum size, and the taxon as a whole is outbred, supplemented by the presence of sporophytic incompatibility. Detailed analysis of the chromosome complement reveals that considerable reshuffling and structural alterations have taken place during the course of domestication, while the analysis of the meiotic system indicates that the complex is segmental allopolyploid in character. DNA estimation in the cultivars shows a direct correlation between ploidy and DNA content. The chief mechanisms underlying evolution are outbreeding, spontaneous and intentional hybridization coupled with mutation, chromosomal differentiation and repatterning and polyploidy.

GARDEN chrysanthemum (*C. morifolium* Ramat.) is an important flower crop throughout the world. According to the recent taxonomic revision, this species complex falls under the genus *Dendranthema*, which is mainly centred in the far east regions like China and Japan¹.

C. morifolium constitutes a polyan euploid complex²⁻⁴ having arisen from a complex hexaploid Chinese species (chiefly two, *C. indicum* L. and *C. morifolium* Ramat. (*C. sinense* Sabine)) through repeated cycles of hybridization and selection extending for over a period of 2,500 years⁵. The present study was aimed at obtaining an understanding of the genetic-evolutionary race history of this important ornamental.

Morphological analysis of cultivars belonging to various horticultural classes has shown that a great deal of variation exists in the floral heads of the cultivars. Based on the capitulum size, two broad classes, viz. the large-flowered (12–17 cm) and small-flowered or Korean (1.9–6.8 cm diameter), have been recognized. Though the size of the capitulum in the cultivar 'Liliput',

having the lowest chromosome number ($2n = 36$), was 2.1 cm, the smallest flower head (1.9 cm) was actually found in a hexaploid ($2n = 54$) cultivar, NN₃. In the large-flowered group the capitulum size varied from 16 to 17 cm in hexaploid, while in octoploid 'Ghenghiskhan' ($2n = 72$) the diameter was only 14.7 cm. Since the size of the flower head can be modified by cultural practices, a strict correlation between this character and the level of ploidy was not apparent. Accordingly, the chromosome number in the small-flowered cultivars tended to fall between $2n = 36$ and 55, that of the large-flowered forms was between $2n = 53$ and 72.

With regard to the breeding system, the capitulum contains two types of florets, outer female ray and inner bisexual disc florets. The head matures centripetally and the flowers are protandrous. Due to conspicuousness as also fragrance of the capitulum, insect pollinators are attracted which affect cross-pollination. However, large-flowered cultivars are seldom visited by insect pollinators, because there is mechanical barrier for pollination due to enormous length of the ray florets and the small size of the pistil. Outbred-

ing is further enhanced by protandry and sporophytic self-incompatibility^{6,7}. It may be pointed out that some degree of self-compatibility is also reported⁶, which is perhaps the result of the breakdown of self-incompatibility during domestication caused by mutation of major genes or 'switch genes' controlling 'S' alleles⁸.

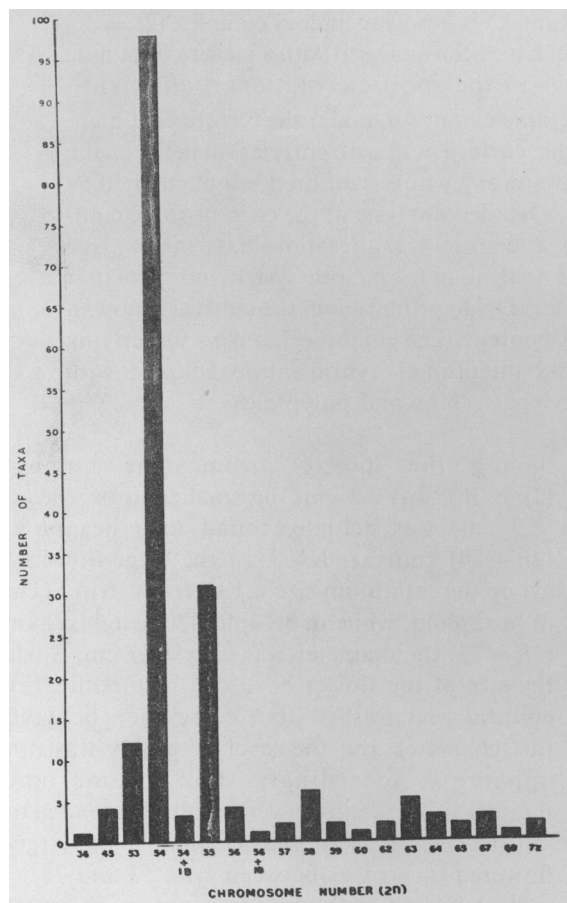


Figure 1. Histogram showing incidence of different chromosome numbers in Indian cultivars of *Chrysanthemum morifolium* complex.

The present detailed analysis of chromosome complement of 183 cultivars, representing different horticultural classes has revealed numbers like $2n = 36, 45, 53-60, 62-65, 67, 68$ and 72 (figure 1). The modal number is $2n = 54$ ($6x$) followed by $2n = 55$ ($6x + 1$) and 53 ($6x - 1$). The cultivars form a continuous series from $6x - 1$ to $8x - 4$, with only two numbers

($2n = 61$ and 66) missing. Further, 4 cultivars showed the presence of one B-chromosome each⁹. However, the total range for the species reported so far is $2n = 36, 45, 47, 51-75$.

There is a decrease in size of the chromosome with an increase in the grade of ploidy. However, DNA content among cultivars varies from 12.64 to 25.33 pg and shows a ratio of approximately 1:1.2:1.5:2 between tetraploid, pentaploid, hexaploid and octoploid respectively. There is a positive correlation between DNA content and ploidy level and the regression is significant ($P < 0.01$) (figure 2)¹⁰.

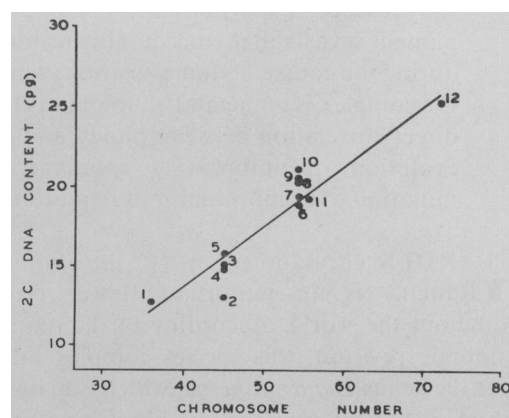


Figure 2. 2C DNA content plotted against chromosome number of chrysanthemum cultivars. 1. 'Liliput'; 2. 'Phyllis'; 3. 'Kasturi'; 4. P_5 ; 5. P_1 ; 6. O_{20} ; 7. 'Nanako'; 8. 'Summer Gem'; 9. 'Megami'; 10. F_5 ; 11. U_2 ; 12. 'Potomac'.

The karyotype is reasonably symmetrical. The basic karyotype could not be ascertained due to lack of marked morphological differentiation between the basic complements in different species. The chromosome complement in most of the cultivars is composed of metacentric, submetacentric and sub-telocentric chromosome. Three cultivars showed the presence of telocentrics in their complement. Irregular meiosis and random segregation of chromosomes lead to tremendous reshuffling of the genome and production of chromosomally unbalanced gametes. However, due to buffering effect of polyploidy, such gametes are not only viable, but also

capable of fertilization and new chromosome combinations and numbers result from their union, which are tolerated⁴. Sporting is another source of variation in the chromosome complement. This is often accompanied by gain or loss of chromosomes due to irregular mitosis in the shoot meristem¹¹⁻¹³. Karyotypic heteromorphicity was observed in the complement of almost all the taxa studied. Such heteromorphicity may rise as a result of pericentric inversion. Small odd chromosomes and abnormally long chromosomes were found in few cultivars, which may appear to have originated through interchanges. Telocentrics present in some cultivars could originate as a result of centric fission, or deletion of short arm in a highly acrocentric chromosome. Owing to small size of the satellite and overcondensation of the nucleolar chromosomes, in some cultivars such chromosomes were not discernible. However, there was no correlation between the number of satellites in a complement and the level of ploidy.

Although the complex forms a polyan euploid series, meiotic analysis in various taxa showed the presence of only a few multivalents accompanied by a very large number of bivalents, indicating segmental allopolyploid nature of the taxa. It is also possible that during the course of domestication, structural alterations as also the resultant recombinations have led to the reshuffling of the genomes with reduced pairing and lower number of multivalents. A few cultivars however exhibited diploid-like meiotic behaviour, characterised by predominant bivalent formation. While anaphase I segregation in most cases was nearly normal, the second anaphase was highly irregular with unequal segregation, lagging, etc. However, pollen stainability was reasonably high (65-90%) and there was moderate seed setting in open pollinated capitula. The high degree of pollen stainability may be due to the polyploid nature of the taxa, with the result that gain and/or loss of chromosomes arising from segregational errors can be well tolerated.

Unlike most of the ornamental plants, garden chrysanthemums have a long history of domestication. The primary centre of origin is China and the Chinese have been growing improved forms

for the last 2,500 years. The garden forms have arisen mainly from two elemental species, *C. indicum* L. and *C. morifolium* Ramat. (*C. sinense* Sabine). The original cultivars were probably single and many-flowered, and during domestication for a long time, there has been a transformation of the corolla of individual florets into numerous forms as seen today. While the first recorded experimental hybrid and the first bud sport arose in 1827 and 1832 respectively⁵, the major improvement of garden cultivars has been accomplished in the gardens of China, Japan, Europe and America through conscious and unconscious selection. In all the above cases, garden chrysanthemums have reached various places in the form of seedlings or seeds. From these stocks new cultivars have arisen as hybrid seedlings and through bud sports. The main evolutionary factor has been indiscriminate intervarietal hybridization by nurserymen and enthusiasts, followed by selection. Further diversity has been brought about by hybridizing with wild species as also spontaneous mutants. The gains accruing through hybridization and mutations have been fixed through vegetative propagation irrespective of the nature and extent of pollen and/or seed sterility.

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